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THE GENETIC RELATIONS OF PLANT COLORS IN MAIZE

R. A. EMERSON

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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R. A. Emerson

Under the designation "plant colors" are included the colors other than those related to chlorophyll, commonly seen in, but not limited to, such external plant parts of maize as the culm, the staminate inflorescence, the husks, the leaf sheaths, and to some extent the leaf blades. In contrast to this group are colors and color patterns related to chlorophyll or associated with the pericarp and the cob, the silks, the endosperm, the aleurone. The colors included in the group considered here are due to water-soluble pigments, but the same is true of some of the other color groups named above. Moreover, colors of the chlorophyll group (Lindstrom, 1918) are found in the same plant parts as are the "plant" colors considered in this account. The plant colors as a whole are closely interrelated, but they are closely related also to aleurone colors and to certain of the silk and pericarp colors. It is obvious, therefore, that, while this classification is a more or less natural one, it is based primarily on convenience.

The term "genetic relations" in the title to this memoir is to include not merely an account of the genetic analysis of the material at hand by means of hybridization experiments — tho that constitutes the greater part of the paper — but also some consideration of the variations of the several color types induced by or associated with environmental diversities. Some little attention to matters of this kind was made necessary by the fact that presumably homozygous material exhibited marked variations in extent and intensity of pigmentation when grown under diverse conditions. Since, as will be apparent later, the principal differences between certain of the color types under investigation are apparently quantitative ones, and since the materials at best exhibit no little complexity with respect to factorial interrelations of a genetic nature, little progress could have been made without some notion of the response of particular color types to certain factors of the environment. But this study has

[1] Paper No. 78, Department of Plant Breeding, Cornell University, Ithaca, New York.

been wholly subsidiary to the main purpose, namely, a genotypic analysis of the color types under observation. The writer's realization of the superficial nature of the environmental studies reported in this account in no way weakens his belief in the importance of acquiring an accurate knowledge of the chemistry of the pigments concerned and of instituting fundamental investigations into the physiology of their development — problems that must await the interest and effort of other workers.

The studies reported here were begun in a small way in 1909 and have been continued, along with other problems in the genetics of maize, to the present time. The work was conducted at the University of Nebraska and supported by funds of that institution from 1909 to 1914. During 1911 facilities for growing and studying a considerable part of the cultures then in hand were generously afforded the writer by the Bussey Institution at Harvard University. Since 1914 the work has been conducted at Cornell University.

During these years, the writer has been assisted by a number of persons, among whom he desires to mention particularly Dr. E. W. Lindstrom and Dr. E. G. Anderson. Some data from the records of students associated with the writer are included in this account. The cultures giving these borrowed data are indicated in the tables by initial letters preceding the pedigree numbers, as follows: A = E. G. Anderson, L = E. W. Lindstrom, and S = Sterling H. Emerson.

The illustrations are from water-color drawings by C. W. Redwood, Miss Carrie M. Preston, and Miss Bernice M. Branson.

PREVIOUS INVESTIGATIONS

So far as the writer is aware, little work with the plant colors of maize has been reported previous to this time. Webber (1906) reported the results of studies of the interrelations of aleurone, silk, anther, and glume colors, with the conclusion that color in all these parts is closely correlated but that there are definite breaks in the correlation. This conclusion, in terms of present-day usage, is apparently equivalent to the idea of close linkage with some crossing-over. East and Hayes (1911) identified certain aleurone-color genes, which are shown in the present account to be related to plant colors as well as to aleurone colors, and reported data concerning the inheritance of silk and anther colors. The writer (Emerson, 1918) added another aleurone-color pair also known to

be concerned in plant-color development. He had earlier (1911) announced some of the plant colors discussed in the present paper and placed on record some evidence as to their genetic behavior. Gernert (1912) described types of maize that differ widely in color of anthers, glumes, silks, sheaths, and husks, and reported simple mendelian behavior in F_1 and F_2 of certain crosses. With this exception, Gernert's extensive investigation of plant-color types has not been reported, but the writer has been able, thru an exchange of material, to compare some of Gernert's types with those in his own cultures.

SOURCE AND DESCRIPTION OF MATERIALS USED

The plant-color types discussed in this paper came in the main from the crossing of two little-known varieties, one of which was obtained at a national corn exposition and the other from an exhibit at a local agricultural fair. One of the color types produced by this cross is the same as that of the dent varieties generally grown thruout the Corn Belt; a second is not infrequently seen in certain pop, flint, and sweet corn varieties; and a third occurs in the fields of flour corn of certain Indian tribes of the Southwest. One of the color types produced by the cross had no existence, so far as the writer knows, until it appeared in his cultures. Modifications of several of the six color types noted above have been produced by crossing with a color type common in a few varieties of sweet corn and closely related to the type most common in field maize. The principal color types concerned in this account are discussed in some detail in the descriptive notes below. They are:

I — Purple
II — Sun red
III — Dilute purple
IV — Dilute sun red
V — Brown
VI — Green

PURPLE, TYPE I

Material of the purple type was first obtained as a single ear from a local agricultural fair at Nehawka, Nebraska, in 1906. The varietal name is unknown. The uncrossed stock was a smooth-seeded pop corn

of medium size. No other stock of purple has been used in the crosses described later in this account, and the writer has never seen this color type in cultivation outside his own cultures. A sample of dent corn of apparently the same color type was seen at a national corn exposition in 1909. A stock of purple was obtained from Dr. Gernert in 1914 but was not used in genetic studies. Another stock of purple was received more recently (1919) from Messrs. Collins and Kempton, the seed having come originally from Bolivia.

Seedlings of the purple type are usually indistinguishable from those of types II, III, and IV (described more fully under type IVa, page 12), altho, unlike the other types, they develop some color when grown in darkness. Half-grown plants of type I usually have the lower sheaths prominently colored, in which respect they exceed type II plants in intensity of pigmentation and are sharply differentiated from types III and IV. At the flowering stage, plants of type Ia have much purple color in nearly all parts, such as the culm, the brace roots, the leaf sheaths, the husks — even the inner ones — the cob, and the staminate inflorescence including the rachis, the spikelets, and the anthers (Plates I, 1, and V, 1). In some cases the color extends over the whole leaf, and it is always seen in the midrib. The purple pigment of type Ia develops in local darkness, as has been shown by covering various parts of growing plants with several thicknesses of heavy black paper (Plate VIII, 1). The color persists in mature plants with slight fading in the outer parts due to weathering (Plate VII, 1). The pericarp of type Ia is either colorless, red, or cherry, and the aleurone is either purple, red, or colorless. With red aleurone the anthers are reddish purple, and with cherry pericarp they are usually very dark purple, almost black (Plate I, 2 and 3).

A subtype of purple known as weak purple, or type Ib, is similar to Ia but the pigmentation is less intense, particularly in the culm and the inner husks (Plate V, 2). In early stages of growth it is often difficult to distinguish Ib from IIa. The anthers of Ib are usually deep purple, as are those of Ia, and the pericarp is the same as for Ia. Another subclass of purple, Ig, is like Ia except that the anthers are green (Plate I, 4) and the pericarp is red or colorless, never cherry. The aleurone color is the same as in Ia.

SUN RED, TYPE II

Sun red, tho not a common color type, is encountered in a few varieties of sweet corn and pop corn. It is always produced in F_2 of certain crosses, notably in purple x green.

While this type is less highly colored than Ia, it has such strong color that it is not easily distinguished from the latter in early stages of growth. At the flowering stage, type IIa is sharply differentiated from type Ia in several respects. The staminate inflorescence of IIa is lighter than that of Ia, and the anthers are deep pink instead of purple (Plate III, 1). In type IIa, pigmentation of the culm, the leaf sheaths, and the husks is limited almost wholly to parts exposed to sunlight, hence the name *sun red*. The inner husks are therefore without red color, and rarely does much color develop in any but the outer layer of husks (Plate V, 3) notwithstanding the fact that sufficient light penetrates to the inner husks to induce the development of some chlorophyll in them. A tassel inclosed in a black paper bag produces no red color in either glumes or anthers (Plate VIII, 4). Since the color of sun red plants is so largely superficial, it disappears almost wholly from mature plants thru weathering (Plate VII, 2). Sun red plants have either red or colorless, but never cherry, pericarp, and either purple, red, or colorless aleurone.

Sun red of type IIg differs from IIa merely in having green instead of pink anthers. Type IIb, known as weak sun red, differs from IIa in the lesser intensity and extent of its pigmentation. Particularly the leaf sheaths and the husks are less highly colored than in type IIa. Often the color of the husks develops in alternate dark and light bars parallel to the upper margins of the overlapping husks (Plate V, 4). Types IIb and IIg have the same pericarp and aleurone colors as IIa.

DILUTE PURPLE, TYPE III

The dilute purple type, as well as the sun red, occurs regularly in F_2 of purple x green, and most of the dilute purple material in the writer's cultures came originally from this and other crosses. It was first observed in the progeny of such crosses in 1909. Recently two stocks of this color type have been received from G. N. Collins, one obtained from the Hopi Indians of southwestern United States and the other from Bolivia.

Seedlings and young plants of type IIIa show no more color than do those of type IVa, and apparently do not develop color in darkness. As the plants approach the flowering stage, they usually show somewhat more color than do plants of type IVa, particularly at the base of the culm and in the brace roots, and sometimes in the leaf sheaths. The staminate inflorescence is usually, tho not always, somewhat more highly colored than that of type IVa. The anthers are deep purple, like those of type Ia (Plate II, 1). With red aleurone the anthers are usually reddish purple, and with cherry pericarp they are dark purple, sometimes appearing nearly black (Plate II, 2 and 3). The anther color develops fully in darkness, but the glumes are slightly if at all colored when protected from light by black paper bags (Plate VIII, 3). As the plants mature, considerable color develops in the inner husks (Plate VII, 3), on the leaf sheaths, and particularly in the culm even where it is protected from strong light by the sheaths. In some cases the culm and the sheaths ultimately become nearly as strongly pigmented as type Ia, but ordinarily the mature plant is considerably less highly colored than the purple type (Plate VII, 4). The color seen in mature plants develops well in local darkness, in which respect also type IIIa is like Ia. Dilute purple differs from purple, therefore, mainly in a less intense pigmentation and in a delayed development of pigment. The pericarp of type IIIa is either red, cherry, or colorless, and the aleurone is either purple, red, or colorless, just as in type Ia.

There exists a type of plant color which is closely related genetically to type IIIa, but which lacks red or purple color in culm, sheaths, silks, glumes, and anthers and is consequently known as *Green, type IIIg* (Plate II, 4). The aleurone of this type is either purple, red, or colorless, and the pericarp is either red or colorless, never cherry. With respect to aleurone and pericarp, therefore, type IIIg is like type Ig.

DILUTE SUN RED, TYPE IV

Dilute sun red is the commonest color type of maize in cultivation. It is practically the only color type seen in the dent varieties grown in the Corn Belt of the United States, and is common in flint, flour, sweet, and pop corns. Like the sun red and the dilute purple types, it always appears in crosses of purple Ia with green VIc.

The seedlings of type IVa usually show more or less sun red pigment in the coleoptile, the leaf sheath, and the leaf margins. The young

plants ordinarily have considerable color at the base of the lower sheaths, but little or no color except green in other parts except in the margins of the leaves (Plate IX, 1). When the plants are grown on infertile soil, much bright red color develops in all parts exposed to light except the youngest leaves (Plate IX, 2). The seedlings and the very young plants are not ordinarily distinguishable from those of types Ia, IIa, and IIIa. Some time before the flowering stage, the plants of this type are sharply differentiated from those of types Ia and IIa, and are usually somewhat less highly colored than those of type IIIa. In normally grown plants, the color is confined mostly to the brace roots, and to the sheaths and the exposed parts of the culm at the base of the plants. Even at the flowering stage almost no color is seen in the upper sheaths or the upper part of the culm, and very little in the husks (Plate VI, 1). The staminate inflorescense is colored much as is that of the sun red type, tho the glumes are lighter than those of type IIa and the rachis is usually nearly devoid of color. The anthers show more or less pink, as do those of type IIa. There is much variation in the extent and intensity of pigmentation of glumes and anthers (Plate III, 2, 3, and 4), due in part to genetic differences and in part probably to environmental influences. Late in the life of the plant, type IVa usually shows some color in the outer husks and also in exposed parts of the culm. Different strains show considerable variation in this respect (Plate VI, 1 and 2). Due to the slight development of pigment and because of weathering, the dry parts of mature plants show little red color (Plate VII, 6). Light is essential to the development of color in dilute sun red, IVa, just as in sun red, IIa. The aleurone and pericarp colors of dilute sun red, IVa, are the same as those of sun red, IIa.

A wholly green type, that is, one devoid of pigment other than green in the plant parts here under consideration, is closely related genetically to type IVa and is therefore known as type IVg (Plate II, 4). Phenotypically it is the same as type IIIg. Just as in case of types Ig, II, IIIg, and IVa, the pericarp of IVg is either red or colorless, never cherry, and the aleurone is either purple, red, or colorless. Genotypic diversities in the amount of color are noted for type IVa above. The lightest types of dilute sun red show no color except mere traces of red in the staminate spikelets. This condition is found in most plants of at least two varieties of sweet corn, Black Mexican and Crosby. From these varieties there

have been isolated strains that lack even this minimum of color. These strains furnished the original stock of type IVg. In no environment as yet encountered has any red or purple plant color developed in type IVg.

BROWN, TYPE V

The brown type was first seen in 1912, when it occurred in F_2 of the cross purple Ia x green VIc. So far as the writer has been able to learn, brown plant color had not been reported previously, and he is unaware of its existence outside of his own cultures or of stocks grown from them.

Seedlings and young plants of type V are wholly green. Before the flowering period is reached, a brown pigment begins to appear in the lower sheaths. At the time of flowering, the culm, the sheaths, the husks (Plate VI, 3), and the staminate inflorescence (Plate IV, 1 and 2) are brown. The anthers are usually green. The brown color extends to the inner husks, to the culm beneath the leaf sheaths, and to the cob (Plate VII, 5). That light is not essential to the development of brown is shown further by the fact that the color appears under several thicknesses of black paper (Plate VIII, 2). It is not uncommon to find traces of purple associated with the brown in the brace roots and at the base of the inner husks (Plate VI, 3). Abnormally developed tassels, not infrequently seen on plants grown in small pots in the greenhouse, in some cases show a little purple (Plate XI). The aleurone of brown plants is always colorless, except for xenia grains, and the pericarp is either brown, brownish, or colorless, never red nor cherry. Brown pericarp color of type V corresponds to red of types I, II, III, and IV, and brownish to cherry of types I and III.

GREEN, TYPE VI

The writer's stock of the green type originated from a single ear obtained at a national corn exposition held at Omaha in 1909. The corn was exhibited from southern Missouri, where it is grown locally. It is a large dent variety, rather late in season.

Cultures of type VIc, derived from this stock, show no plant color other than green at any stage of development or under any environmental conditions to which they have as yet been subjected (Plates IV, 3, and VI, 4).

Three subclasses of type VI are recognized. One of these, VIa, is like VIc in every respect except that a slight amount of brown is sometimes seen in the outer husks and sheaths (Plate VI, 5). The second, VIb, is green except for a slight tinge of brown in the spikelets of the staminate inflorescence (Plate IV, 4). As a rule, the development of brown pigment in VIa and VIb is not sufficient to differentiate with certainty the one from the other, or either from VIc. The three subclasses, a, b, and c, are therefore usually classed together as type VI. Both VIa and VIb have been isolated from crosses involving VIc. The aleurone of all type VI plants, just as in those of type V, is colorless, except for such color as may be due to xenia. The pericarp of VIa and VIc is either brown or colorless, never brownish, while that of VIb is brown, brownish, or colorless, as in the case of type V. With brownish pericarp, type VIb usually shows unmistakable brown color in the staminate spikelets.

RELATION OF PLANT COLORS TO ENVIRONMENT

From the preceding descriptive notes and accompanying illustrations, it is clear that many of the differences separating the six major color types and their several subclasses are quantitative. Purple plants are more strongly colored than are sun red or dilute purple plants. Dilute sun red plants have less color than sun red or purple plants. Weak purple plants have less color than purple ones, but more than dilute purple ones, and weak sun reds are intermediate between sun reds and dilute sun reds. Dilute sun red plants vary, from those showing considerable color to those which, except for green, are nearly colorless. Wholly green plants are classed as subgroups of both dilute purple and dilute sun red. The subclasses of type VI differ so little with respect to color that they are ordinarily thrown together as one green type. Heterozygous brown plants are lighter than homozygous ones, and, since more than one factor pair is concerned, there is a fairly smooth gradation from the darkest to the lightest browns. Plants of types VIa and VIb, when they show any brown, differ in the parts colored. The color of the staminate inflorescence, and even of other parts, of purples, dilute purples, browns, and greens of type VIb is darker when the pericarp is cherry or brownish than when it is red, brown, or colorless.

The natural intergrading of genetic types in this somewhat complex series is often made still more confusing by the variations accompanying

environmental diversities. A prominent geneticist, on observing some of the writer's cultures, was led to say that there were no sharply differentiating characteristics by which other than an arbitrary classification could be made, and asserted that he could select from a single progeny a series grading from the darkest to the lightest colors. The writer has some doubt that this could have been done, but the instance illustrates well the difficulties that confront one unacquainted with the materials. It is fortunate that some environmental influences which increase the difficulty of assorting certain color types make other types stand out more sharply than they otherwise would. Without some notion of these environmental effects, a genetic analysis of the material would indeed be difficult.

SUNLIGHT A FACTOR IN COLOR DEVELOPMENT

The relation of sunlight to the development of color has been noted briefly in the descriptions of some of the color types. The effects of sunlight or of local darkness, instead of adding to the confusion of color types, afford a means of sharp differentiation between certain types. So far as is known at present, no color develops in sun red or dilute sun red plants, or in the early stages of growth of dilute purple plants, except under the influence of fairly strong light. In the case of purple and of the later stages of growth of dilute purple, there is no doubt that the color develops more rapidly at first in light than in darkness, but ultimately color develops fully, or apparently so, even in local darkness (Plate VIII). The seedlings of purple plants develop some color when germinated and grown in a dark chamber where no part of the plant receives light. There is some, tho very little, evidence that the development of brown pigment of type V is hastened by the influence of light, and what little brown color ever develops in type VIa is confined to parts exposed to sunlight (Plate VI, 5).

It would not be surprising to find that the pigments seen in the purple, dilute purple, sun red, and dilute sun red types are the same chemically. In fact they look alike in water solution and apparently react in the same way to simple chemical tests. If they prove to be identical, it would seem to follow that purple and dilute purple plants have some inherent mechanism, perhaps an organic catalyzer, capable of initiating or hastening chemical reactions, and that this mechanism is lacking in sun red

and dilute sun red plants, in which the same reactions may possibly be brought about thru the action of sunlight.

Usually a single thickness of black paper, such as is employed to protect photographic plates from light, is sufficient to prevent the development of color in sun red plants (Plate VIII, 4). That more intense light is necessary for the production of sun red pigment than for the production of chlorophyll is shown by the almost entire absence of red color in all but the outer husks, while even the innermost husks are somewhat green (Plate V, 3). The pigments of purple and brown plants, on the contrary, develop well even when there is too little light for the formation of chlorophyll (Plate VIII, 1 and 2).

That the effect of light on color development is a definitely local one is shown by the sharp line of demarcation between colored and colorless areas in culms, husks, and sheaths partly exposed and partly protected by overlapping sheaths or husks (Plate V, 3). Even a single piece of wrapping cord tied closely about a young ear, sheath, or culm of a sun red plant is sufficient to prevent the development of color beneath it. Evidently sun red pigment does not diffuse appreciably from the cells in which it forms. It is not meant to suggest by these observations that sunlight has no effect other than a local one on color development. On the contrary, there is evidence that the development of sun red color is influenced by the presence of an abundance of carbohydrates which in turn are dependent on sunlight for their formation.

A striking example of the relation of sunlight to color development is afforded by the barred pattern seen in the husks of some weak sun red plants (Plate V, 4). The pattern consists of alternate bars of red and green parallel to the upper margin of the overlapping husk next below them. By tracing in pencil on each exposed husk of a rapidly growing ear the margin of the husk overlapping it, it has been ascertained with certainty that the red bars correspond to the areas that are pushed out from under the overlapping husk between early morning and late afternoon, while the green bars correspond to the areas pushed out during the late afternoon and night. Why color develops in only those parts of the husk that receive the sunlight when first exposed to the air, and not in the parts exposed some hours previously, is not known. Another illustration of the effect of sunlight on freshly exposed husks was seen in a very light type of weak sun red (Plate V, 5). Of two ears on the same culm, both very lightly

and about equally colored, the lower had its husks torn apart in the early forenoon so that the fresh inner husks were exposed at once to direct sunlight. In a few hours some red color began to show, and in a few days all the newly exposed husks were brilliantly colored, while the undisturbed upper ear remained only slightly colored. Similar results followed in repeated trials, and, in fact, failed only when the atmospheric conditions were such as to cause the newly exposed husks to wither during the first day. It is of interest to note also that similarly treated ears of dilute sun red plants, which rarely show any red color in the outer husks of young ears, failed to develop color when the husks were torn apart, even tho they remained fresh for some days.

It is evident from all this, that, with respect to their relation to sunlight, there exists a series of color types varying more or less abruptly from dilute sun red, in which little or no sun red develops in even freshly exposed husks, thru weak sun red, in which color forms in only freshly exposed husks, and strong sun red, in which much color develops in all exposed parts of the husks but not in parts protected from light, to strong purple, in which, tho sunlight may hasten color development, it is not essential to its formation.

Tests of the influence on color development of light of different wave lengths have not been uniformly successful. Cramer photographic color screens were placed in partial contact with the uncolored inner husks of sun red plants, and the entrance of light otherwise than thru the screens was prevented by means of strips of black paper. These screens, by cutting out light of certain wave lengths, not only change the quality of light passing thru them but lessen the intensity of the light. While the results, therefore, can have little value, it may be of interest to physiologists to note that considerable sun red formed under the orange and the bright red screens, and little or none under the green and the blue screens.

MOISTURE IN RELATION TO COLOR

It is well known that under field conditions maize does not grow well in wet soil. In such situations, not only are the plants small, with their leaves pale green, but they often develop much red pigment. The writer has repeatedly observed that young plants, in flooded parts of fields where the soil had been covered with water for some days, were brilliantly red in all parts except the youngest leaves, while near-by plants on slightly

higher land showed only the slight red at the base of the culms characteristic of young dilute sun red plants.

For a study of the effect of soil moisture on color development under controlled conditions, plants of well-known stocks of purple Ia, sun red IIa, dilute purple IIIa, dilute sun red IVa, brown V, and green VIc and IVg, were grown in rich soil in earthen jars in the greenhouse during the summer of 1914. When the plants had reached a height of from 10 to 15 centimeters, the jars were separated into three lots — one with dry soil, another with moist soil, and a third with wet soil. The dry-soil lot received only sufficient water to keep the plants growing slowly and not enough to prevent wilting during the hotter part of the day. The moist-soil lot received just sufficient water to insure normal growth. The wet-soil lot was kept constantly in saturated soil with some free water above the soil surface. The test was continued until the plants of all lots reached the flowering stage.

The plants in moist soil made the most rapid growth and flowered somewhat earlier than the plants of the other lots. Their leaves were of normal green color and they showed the colors characteristic of the several color types. The plants in dry soil were smaller and very dark green. The development of purple, red, and brown color was practically the same as with the plants in moist soil. The plants in wet soil grew less rapidly than those in moist soil, but more rapidly than those in dry soil. Their leaves were somewhat lighter green than those of the moist-soil lot, but they showed practically the same amount of purple, red, and brown color. In fact the only differences between the three lots with respect to color at any time during the test were such as might well be related to the stage of development of the plants. All color types show more color in the later stages of growth. The moist-soil lot developed somewhat more rapidly than did the others and for a time showed slightly more color, but ultimately all lots had practically the same amount of color. Evidently the reddening of plants in flooded fields is not due directly to the excess of soil moisture.

TEMPERATURE IN RELATION TO COLOR

Since moisture is not the direct cause of the reddening of maize plants in flooded fields, tho certainly connected with the phenomenon in some way, it follows that the effect must be produced by some indirect action

of the excess of water. Wet soils in spring are cold soils, and if the wet areas are of considerable extent the air above them is doubtless somewhat cooler than that above drier soil. It has been frequently observed that young plants which show much color during a cold spring show considerably less in the leaves developed after the weather has become warmer. Young plants of early-planted maize sometimes have more color than plants that are started later. Moreover, full-grown plants from late plantings often develop more color in the cool weather of autumn than similar plants that mature in the warm weather of late summer. It seemed important, therefore, to study the effects of various temperatures on color development.

The same color types and the same stocks— in one test the identical plants— used in the soil-moisture test were grown in the greenhouse under diverse temperatures. Altho both rich and poor soils of diverse water content were used, the comparisons noted here were made between plants in the same kind of soil and with practically the same soil-moisture conditions. Two lots were grown during the winter of 1913–14 and two during the following summer. During the winter, one lot was kept in a warm house at temperatures varying from about 18° to 26° C., and one was kept in a cool house at temperatures varying normally from about 7° to 15° C. but during a part of the test dropping at night to 1° or 2° C. Both lots were exposed to the full winter sunlight of the houses. During the summer test, one lot was kept as cool as possible by partial shading and free ventilation, the temperatures ranging from about 15° to 40° C. but occasionally exceeding these limits, and the other lot was kept in an unshaded house the ventilators of which were never opened. The night temperatures of the closed house averaged not more than one degree higher than those of the open house, but the maximum day temperatures in the closed house varied usually from about 44° to 50° C. and on three consecutive days reached 55° C. This extreme heat killed most of the plants grown in rich soil but did not seriously injure those in poor soil. Of course the relative humidity, as well as the intensity of the light, was materially different for the closed and the open house.

As a result of these tests, no final differences in the development of color in any of the color types were observed between the lots grown at the very diverse temperatures. Of course differences were observed at certain times, but they are readily accounted for by the facts that the

plants developed less rapidly at both excessively high and excessively low temperatures than at more moderate temperatures, and that color shows less during the early stages of development than during later stages. It may be safely concluded, therefore, that color development in maize is not notably influenced, except perhaps indirectly, by diverse temperatures.

SOIL FERTILITY AND COLOR DEVELOPMENT

There is still another way in which it was thought the excess of water might indirectly affect the development of color in maize plants in flooded fields. Not only may nutrient salts be removed in part by an excess of water, but certain of these salts — nitrates — are not formed normally in very wet soils. Tests were made, therefore, of the relation of soil fertility to color development.

Rich compared with poor soil

The same plant-color types as were employed in the soil-moisture and temperature tests were included in these soil-fertility tests. In fact, for one of the tests the same plants were used as in the moisture and temperature studies. One lot of plants was grown in rich soil and a duplicate lot in poor soil. Field soil furnished the basis of both soils. To one lot was added about 50 per cent by measure of thoroly decayed stable manure, and to the other about 50 per cent of clean sand.

The effect of soil fertility on color development of certain color types was strikingly apparent from the time the seedlings were two or three weeks old. At this age and for some time later, there was no appreciable difference in color between purples, sun reds, dilute purples, and dilute sun reds. In the rich soil all these color types had very little red color. There was some color in the coleoptile and the lower leaf sheath, but none in the leaf blades except for a slight amount in their margins. The same color types in poor soil had considerable color in the leaf blades and much color in the leaf sheaths. The plants in rich soil grew rapidly and were dark green, even the lower leaves remaining healthy. The plants in poor soil, on the contrary, grew less rapidly and were lighter green, and their lower leaves soon became yellow and died. In all cases the leaf blades became brilliantly red before they died. This is in strong contrast with the condition of the lower leaves of plants in dry, rich soil. When the

death of the lower leaves is caused by drouth, there is no corresponding development of red color.

At the age of six weeks, the plants in rich soil were beginning to show slightly the color differences that in later stages are characteristic of purples, sun reds, dilute purples, and dilute sun reds. In poor soil, on the contrary, no color differences were seen. All the four types were highly colored thruout except for the youngest leaves (Plate IX, 1 and 2).

At the flowering period, the plants in rich soil exhibited all the peculiarities of color by which purples, sun reds, dilute purples, and dilute sun reds are normally differentiated. Even in the poor soil something of the same color differences were discernible between the purples and sun reds on the one hand and the dilute purples and dilute sun reds on the other, but it is doubtful whether these two groups could have been separated accurately from a mixed culture. It would have been very difficult also to separate with certainty the purples from the sun reds or the dilute purples from the dilute sun reds, except by differences in anther color and by an examination of the inner husks and other parts protected from sunlight. Differences between the plants in rich and in poor soil were still pronounced in the case of dilute purples and dilute sun reds, but were scarcely discernible in the case of purples and sun reds except that the leaf blades were somewhat more highly colored with poor than with rich soil and that thruout the plants the colors appeared brighter in the former case owing to the less intense green of the poor-soil lots.

The seedlings of both brown and green color types showed no brown nor red color in either the rich or the poor soil. At the age of two months, some brown pigment began to show in the lower sheaths of the brown type, and at the flowering stage the plants had the typical coloration of brown plants. The difference in the development of brown between rich and poor soil was at no time very noticeable. The color showed perhaps slightly earlier, and was perhaps slightly more intense, with the poor soil. Even this apparent difference, however, may have been due merely to the fact that the plants in poor soil were lighter and more yellowish green than those in rich soil. Dark green might readily mask the brown color somewhat. Green plants of both type VIc and type IVg exhibited no red nor brown color at any stage of development in either rich soil or poor soil.

From these observations it is apparent that variations in soil fertility may effectively obscure genetic differences. A knowledge of the influence of soil fertility on color development is therefore essential to careful genetic work with the plant colors of maize. Moreover, since soil fertility is subject to control thru cultural methods, different degrees of fertility can be used as an aid to the sharp differentiation of certain genetic types. If, for instance, it is desired to separate, in the seedling stage, greens and browns on the one hand from the red-purple series on the other, this can be accomplished most readily in poor soil. In fact, the writer's practice, in studies requiring this separation, is to grow the seedlings in pure sand. In this medium seedlings of the purple-red series of color types become highly colored at a very early age, while seedlings of the green and brown types show absolutely no red color. If, however, it is desired to distinguish sharply between purple and dilute purple or between sun red and dilute sun red, fairly fertile soil is essential, and, usually, the more fertile it is, the more easily can the separation be made. The stronger colors develop almost as well in rich as in poor soil, while the weaker colors develop much less intensely in rich soils than in poor ones. On very poor soils, it is difficult to separate sun reds from dilute sun reds, and almost if not quite impossible to distinguish with certainty between sun reds and weak sun reds or between weak sun reds and dilute sun reds.

Lack of particular nutrient elements

It having been established that differences in soil fertility result in marked differences in the development of red color in maize plants, it seemed important to determine whether particular nutrient salts are more concerned than others. Accordingly, plants of all the color types included in the tests previously reported were grown in glazed earthen jars in clean quartz sand and watered with nutrient solutions. The quartz sand was obtained from the Department of Agronomy of the University of Nebraska, and was known to be practically free from nutrient elements except iron. The nutrient salts and distilled water were obtained from the Department of Agricultural Chemistry of the same institution. The nutrient solution employed was one that had given good results with maize in certain experiments conducted previously by the Department of Agronomy. The complete nutrient solution, 0.2 per cent strength, contained per liter of water the following salts: 1 gram $Ca(NO_3)_2$, 0.25

gram KNO_3, 0.25 gram K_2HPO_4, 0.25 gram $MgSO_4$, and 0.25 gram NaCl. Other solutions of approximately equivalent molecular strength, but each lacking one of the nutrient elements of the complete solution, were used. In the nitrogen-free solution, 0.7 gram $CaCl_2$ and 0.22 gram K_2SO_4 were substituted for $Ca(NO_3)_2$ and KNO_3, respectively; in the phosphorus-free solution, 0.25 gram K_2SO_4 for K_2HPO_4; in the potassium-free solution, 0.2 gram $NaNO_3$ and 0.2 gram Na_2HPO_4 for KNO_3 and K_2HPO_4, respectively; in the calcium-free solution, 1 gram $NaNO_3$ for $Ca(NO_3)_2$; in the magnesium-free solution, 0.3 gram Na_2SO_4 for $MgSO_4$; and in the sulfur-free solution, 0.2 gram $MgCl_2$ for $MgSO_4$. A complete nutrient solution of four times the strength indicated above, 0.8 per cent, was also used, and one lot was given water without the addition of nutrients. After the first three weeks, the nutrient solutions were all used at double strength, 0.4 and 1.6 per cent, and clear water was occasionally given. This treatment, owing to considerable evaporation of water, doubtless resulted in a gradual increase in the strength of the solutions. The tests were carried on at the same time with one of the tests of rich and poor soil, so that the latter might serve as a check on the nutrient-solution tests.

At first the seedlings given 0.2-per-cent complete nutrient solution reacted about as did those in poor soil, while those given 0.8-per-cent nutrient solution were no more highly colored than those in rich soil. At one month of age, the plants watered for three weeks with 0.2-per-cent and one week with 0.4-per-cent complete solution were growing rapidly and were no more highly colored than those in rich soil, while the plants in the very strong solutions (0.8 and 1.6 per cent) were beginning to wilt, perhaps from the toxic effect of the solutions. Thruout the remainder of the test, the plants given 0.4-per cent solution, alternated occasionally with clear water, were practically like those growing in rich soil both as respects vigor of growth and color development.

In striking contrast to the plants given complete nutrient solution were the ones given clear water and those in nitrogen-free nutrient solution. Both these lots showed much color even at two weeks after germination, and soon thereafter the seedlings were red to the tips of their leaves. At the age of six weeks the plants of these two lots were much shorter and slenderer than those given complete nutrient solution. Their upper leaves were pale yellowish green, with much red, and the lower leaves were dead but still showing the red color that had developed earlier.

Next in point of coloration to the seedlings given nitrogen-free nutrient solution and those given water alone, were the ones grown in phosphorus-free nutrient solution. The latter did not show red color so quickly as did the nitrogen-free lot, and at no time did they develop quite so much color. They showed, however, considerably more color at the age of one month than did seedlings in the complete nutrient solution. When six weeks old the plants of the phosphorus-free lot were relatively small, and had pale green upper leaves with little red color and dead lower leaves which still retained much red pigment. While somewhat larger than the plants in nitrogen-free solution and those in clear water, the phosphorus-free lot began wilting when about six weeks old and died considerably in advance of the nitrogen-free lot. Their roots showed early indications of injury, perhaps from toxic effects of the solution.

Plants of all the other lots, in which one or another nutrient element had been omitted from the solution, exhibited little or no color reaction to the lack of a particular element. All of them were more vigorous in growth than the nitrogen-free and phosphorus-free lots, but much less so than the lot given complete nutrient solution. The sulfur-free lot for a time seemed to be developing more red, but later showed perhaps even less red, than the lot with complete nutrient solution. The magnesium-free lot showed prominent dark and light green stripes in the leaves similar to the green-striped chlorophyll pattern (Lindstrom, 1918). In some cases the tissue of the lighter stripes died and there was often some red coloration next to the dead tissue. The potassium-free lot had about the same amount of red color as the lot given complete nutrient solution, while the calcium-free lot showed less red color than any other lot in the test.

It is perhaps noteworthy that in the nitrogen-free lot, and to some extent in the phosphorus-free lot, the new growth seemed to take place at the expense of the older leaves. The lower leaves first became light or yellowish green, then red, and finally died. That the development of red pigment is not necessarily connected, however, with the breaking down of the protoplasm, is seen in the failure of seedlings to develop red color in the older dying leaves of the lot in complete nutrient solution and of the potassium-free, magnesium-free, and calcium-free lots. In the calcium-free lot, growth was stopped by the death of the youngest parts, including the partly unrolled upper leaves, and yet these parts showed

no red. Moreover, the dying of the lower leaves due to excessively dry soil, or of the upper leaves from intense heat, is not accompanied by the development of red pigment.

In similar tests with cuttings of *Tradescantia viridis* and *T. lockensis* grown in distilled water, in complete nutrient solutions, and in solutions each lacking one nutrient element, namely, N, P, K, Ca, Mg, or S, Czartkowski (1914) found that after five weeks red color appeared in the newly developed leaves in the cases of only distilled water and nitrogen-free solutions. He states, however, that Susuki reported a similar effect on plants of Hordeum from a lack of phosphorus. It will be recalled that in the writer's tests with maize, lack of nitrogen gave the most pronounced effect and lack of phosphorus induced considerable color development, while lack of sulfur seemed for a time to have an effect but no effect was apparent later.

From the results of the tests reported above, it is apparent that the reddening of young plants in flooded fields, as well as the intensification of color in older plants grown on poorly drained heavy soils, is not due to any direct effect of the excess of water in the soil or to a direct effect of the somewhat lower temperatures accompanying such conditions, but rather, perhaps, to the lessened fertility of cold, wet soils or to inability of the plant to obtain adequate nutrients under such conditions. An excess of water not only may remove certain nutrient salts from the soil, but also may prevent or greatly check nitrification. Moreover, under these conditions the soil solution is probably less concentrated. The reddening of young plants in cold, wet soils in spring, the greater development of color in plants maturing in the cool weather of late autumn, and the excessive development of red in plants on very light sandy soils, are possibly all due to the plants' inability to get from such soils an adequate supply of nutrient salts, particularly of nitrates.

RELATION OF CARBOHYDRATES TO COLOR

Several authors, notably Wheldale (1911), have discussed the relation of sugars to the production of anthocyanins in plants. Knudson (1916: 24, 62) found that maize and vetch grown in nutrient solutions containing certain sugars developed markedly more red color than did plants grown in sugar-free solutions. The writer has observed repeatedly an apparent relation between an excess of carbohydrates and the development of red

color in maize leaves. Of course the relation has been observed only in types that normally produce some red pigment. Neither brown, type V, nor green of either type IVg or type VI, has ever been observed with red color in the leaves, no matter what treatment has been given the plants. When leaves are folded at right angles to the midrib and the margin of the fold is creased sufficiently to break the softer tissues but not enough to break the water-conducting vessels, the part beyond the crease does not wilt, but within a few days it begins to lose some of its chlorophyll and within a week it becomes highly colored red (Plate X, 1). When leaves are similarly treated late in the afternoon of a bright day and the plants are kept in a dark room until the following day, the starch is, of course, found to have disappeared by translocation from the part of the leaves below the crease, while the cells of the bundle sheaths of the part beyond the crease are found to be packed with starch. There is so much starch in this part of a creased leaf that, on extraction of the chlorophyll with alcohol and treatment with iodin, the whole end of the leaf becomes almost black. While this does not prove a direct relation between an excess of carbohydrates and the development of red pigment, taken in connection with all the other observations it strongly suggests such a relation.

It has been observed repeatedly that sweet-corn plants from which the ears have been removed in the edible stage develop within a week or two much more color than do neighboring plants that still retain their ears. Barren stalks also frequently show more color than do their ear-bearing neighbors. While no direct determination of the matter has been made it seems likely that barren plants, as well as plants from which the immature ears have been removed, may carry, in their leaves, husks, and culms, an excess of carbohydrates which would normally have been deposited in the developing seeds.

The strong development of red pigment in the white, chlorophyll-free stripes of the japonica-striped type, when leaves are creased or when plants are grown in poor soil, may well be due to the passage of sugars from the green to the white parts. In some instances the red color seems to develop more quickly in the white stripes than in the green (Plate X, 2). Whether this difference is a real one, due perhaps to the readier access of light to the white parts, or is only an apparent difference due to the

masking effect of the green color, is not known. Certainly red pigments develop first in the chlorophyll-free epidermal cells.[2]

Czartkowski (1914) suggested, in connection with the account of his study of the relation of nutrient elements to color development, that lack of nitrogen may check protein synthesis, thus leaving unused the carbohydrates that would otherwise be used in growth, and that the excess of carbohydrates may favor anthocyanin formation. He was unable to understand why a lack of phosphorus or of sulfur did not likewise influence color development, since these elements also are necessary to protein synthesis. Lack of phosphorus does apparently bear some relation to color development in maize, but the writer's tests afforded little or no evidence of such a relation between a lack of sulfur and pigment formation. If lack of nitrogen induces anthocyanin formation thru the checking of growth, thus allowing an accumulation of carbohydrates, it is not clear why other means of checking growth, such, for instance, as dry soil, do not also favor pigment formation, unless these other growth-checking factors at the same time limit photosynthetic activity. It is of interest to recall in this connection that plant colors of maize — brown no less than the red-purple series — develop first in the older parts where growth first ceases, such as the lower sheaths and the upper parts of the internodes of the culm.

SUMMARY

Whatever is the final outcome of studies of the relation of environmental factors to plant-color development in maize, enough has been noted to indicate a very complex relation. What is more complex than this chain of events — a chain that lacks many links in the way of particular chemical reactions: cold, wet soil checks or inhibits nitrification; lack of nitrogen in available form limits protein synthesis, which in turn allows an accumulation of carbohydrates; an excess of carbohydrates favors anthocyanin formation. The result is that young maize plants in cold, wet soil become highly colored. But to all this must be added the factor of sunlight, without which no red color develops in the leaves of young plants. And not the least consideration is the important fact that only plants of certain genetic constitutions show this color reaction to wet soils. It is to be hoped that some day, thru the coordinated efforts of

[2] The histology of color development of the several plant-color types has been investigated by Dr. E. G. Anderson, but the observations have not been published.

biochemists, physiologists, and geneticists, it may be possible to reach conclusions in this field of quite as fundamental importance to biology as the recent results of similar efforts of cytologists and geneticists.

GENETIC ANALYSIS OF COLOR TYPES

In the preceding parts of this paper the several plant-color types of maize are described and the variations induced in them by diversities of environment are discussed. The remainder of the paper is devoted to a presentation of data of a more distinctly genetic nature, and to an attempt at a factorial analysis of these data.

The data are presented as if the F_2 generation of the more complex crosses were the first which were obtained and on which hypotheses were formulated and appropriate tests made. As a matter of fact, this was not in all cases the actual procedure. In several instances the results of some of the simpler crosses were at hand and were used as an aid to the interpretation of the more complex ones when the latter were obtained. Moreover, the hypothesis presented here was not the only one, nor indeed the first one, formulated. As is usual in such work, various hypotheses were devised, tested, and discarded, until finally a factorial interpretation was found that fitted fairly well all the facts known. Many results with a bearing on plant color were obtained in other studies extending over a period of some eight or nine years. Since the practice of the writer is to number his pedigrees consecutively from year to year, an inspection of the pedigree numbers, as listed in the tables, suggests at once that some of the data presented as checks on other results could not have been obtained after these other results. Any data applicable as a test have been so used whether obtained for that purpose or in connection with other studies. Whether this mode of presentation is the best one must be left to the judgment of others. This at any rate is certain: the data could not have been presented chronologically and discussed in relation to such hypotheses as happened to be under test at the time any particular results were obtained, without adding unnecessarily to the complexity of the paper.

CROSSES INVOLVING THE FACTOR PAIRS *A a, B b, Pl pl*

Purple Ia x green VIc

Generations F_1 and F_2.— When purple plants with purple anthers (type Ia) are crossed with plants lacking all red, purple, or brown

pigment, commonly known as green (type VIc), the F_1 offspring are full purple. Whether or not a quantitative determination of purple pigment might reveal a difference, no dilution of the purple color is apparent to the eye in the F_1 plants. Four crosses of this sort with a total F_1 progeny of 111 purple plants are listed in table 1 (appendix, page 121).

Seven F_2 progenies of the F_1 plants recorded in table 1 are listed in group 1 of table 2. Fourteen other similar F_2 progenies are shown in group 2 of the same table. The F_1 plants from which these fourteen F_2 progenies came are not recorded in table 1 because their purple parents were not homozygous. Some of the purple plants used as parents in these crosses were F_1's of the original cross of purple with green. Others were from F_1 or some later generation of other crosses having the purple type as one parent. In every case the other parent was a green plant of type VIc. Since the purple F_1 plants of these crosses were presumably the same genotypically as the F_1's shown in table 1, their F_2 progenies may well be included tentatively with those of group 1 of table 2. Each of the twenty-one F_2 lots exhibited six distinct classes of plants with respect to color. The 2117 plants were distributed among the six classes as follows:

Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
952	305	275	91	278	216	2,117

Obviously no simple 3:1 mendelian behavior is in evidence here. Moreover, only four classes are expected in dihybrids where dominance is exhibited. With dominance trihybrids ordinarily give eight classes in F_2 in the well-known numerical relation of 27:9:9:3:9:3:3:1, while only six classes were observed. Inspection of the distribution of the 2117 individuals given above, however, suggests the possibility of a 27:9:9:3:9:7 relation, which should be realized in a trihybrid if the last three classes were indistinguishable. A comparison of observed numbers with those expected on this hypothesis follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Observed	952	305	275	91	278	216	2,117
Calculated[3]	893	298	298	99	298	232	2,118
Difference	+59	+7	—23	—8	—20	—16	—1

[3] In this and most of the following comparisons, the theoretical distributions are calculated to the nearest whole number.

There are rather large differences between observed and expected numbers. The purples are considerably, and the sun reds slightly, in excess of expectation, while each of the other four classes has too few individuals. The probability that these deviations may be due to chance is approximately 0.11. One might expect, therefore, to encounter chance deviations of the magnitude observed here about once in nine such trials. This, of course, does not substantiate the three-factor hypothesis, but merely indicates that it is not necessarily out of keeping with the observed facts.

Backcrosses with green VIc.— A better criterion perhaps is afforded by the backcross of F_1 purples with the green parent type. Records of such crosses are shown in table 3. The backcrosses with F_1's of table 1 are listed in group 1, and backcrosses with similar F_1 purples of other lots in group 2. The same six phenotypes observed in the regular F_2 generation occurred here also. On the basis of the three-factor hypothesis and with the assumption that there are three sorts of greens indistinguishable from one another, the individuals of this backcross should be distributed equally to five classes with the sixth class containing three times as many individuals as any other class. The observed distribution of the 1317 individuals of the fourteen progenies is here compared with the expected distribution:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Observed.....	170	160	176	160	172	479	1,317
Calculated.....	165	165	165	165	165	495	1,320
Difference.....	+5	—5	+11	—5	+7	—16	—3

While a few of the backcross progenies listed in table 3 exhibit considerable deviations from the expected distribution, the fourteen lots taken together approximate it closely. The probability that the observed deviations may be due to chance in random sampling is about 0.85. Deviations as great as these are to be expected thru chance alone, therefore, in about six out of seven trials.

Working hypothesis.— To the three factor pairs used to interpret the results here reported, the symbols *A a*, *B b*, and *Pl pl* have been assigned. The gene *A* is an anthocyanin factor. In the presence of *a a* ordinarily no anthocyanic pigment develops, tho brownish, or flavonol (Sando and Bartlett, 1921), pigment may be formed. The pair *B b* is named for its

connection with the development of brown pigment, tho when both *A* and *B* are present, sun red pigment is produced. The pair *Pl pl* is so termed because of its relation to purple pigment. The phenotypic formulae assigned to the several classes of plant color under consideration here are as follows:

A B Pl — Ia, purple
A B pl — IIa, sun red
A b Pl — IIIa, dilute purple
A b pl — IVa, dilute sun red
a B Pl — V, brown
a B pl — VIa
a b Pl — VIb } green
a b pl — VIc

Obviously the hypothesis in accordance with which the above factorial assignments have been made is subject to several genetic tests. Naturally the first tests to suggest themselves are studies of the behavior of the several F_2 types in F_3 and later generations. Next in order are intercrosses between the several classes. For reasons that will appear shortly, one of these intercrosses is here dealt with before consideration is given to F_3 generations from the several F_2 classes.

Dilute sun red IVa x brown V

From an examination of the factorial assignments listed above, it is evident that crosses of dilute sun red, *A b pl*, with brown, *a B Pl*, should produce purple F_1 plants, *A B Pl*. Moreover, these F_1 purples should be heterozygous for all three factors, *A a B b Pl pl*, just as was assumed for the original cross of purple, *A B Pl*, with green, *a b pl*. The F_2 and later behavior of this cross should also, barring linkage, be like that of the original cross, so that the two can most conveniently be considered together.

Generations F_1 and F_2.— The F_1 generation of twenty-six crosses of dilute sun red with brown plants is given in table 4 (page 123). The dilute sun red parent plants were chosen from any convenient lots known to be homozygous with respect to *A*, *b*, and *pl*. The brown parent plants, on the other hand, were from the F_2 and later generations of the original cross of purple and green or from other crosses. It was to be expected, therefore, that some of the brown plants would be homozygous for both *B* and *Pl*, and some would be heterozygous for *B*, some for *Pl*, and some

for both *B* and *Pl*. This expectation was fully realized. In group 1 of table 4 are recorded the progenies of nine crosses with a total of 263 individuals. All but one plant of the lot were purple. The one dilute sun red plant was presumably due to accidental pollination of the dilute sun red mother plant. Since the dilute sun red parents of all these crosses were *A A b b pl pl*, the brown parents of the crosses listed in group 1 must presumably have been *a a B B Pl Pl*. Similarly, the seven crosses listed in group 2 gave purple and sun red plants only, 143 of the former and 147 of the latter. Evidently the brown parents of these crosses were *a a B B Pl pl*. Again, the six crosses shown in group 3 gave 105 purple, 123 dilute purple, and no other plants. The brown parents of the crosses were therefore, presumably, *a a B b Pl Pl*. Finally, the four crosses listed in group 4 gave 9 purple, 11 sun red, 19 dilute purple, and 17 dilute sun red. The brown parents of these four crosses are assumed, consequently, to have been *a a B b Pl pl*.

The F_2 results from the purple F_1 plants of these crosses of dilute sun red with brown are recorded in table 5. Fourteen progenies of the F_1 plants listed in table 4 are shown in group 1 of table 5, and five progenies from similar F_1 plants not listed in table 4 are entered in group 2. Here, just as with the results of the cross of purple with green (table 2), fairly marked discrepancies between theory and observation appear when the several progenies are taken separately. When, however, the nineteen progenies are considered together, very close agreement is found between observation and expectation, as is shown by the comparison below. The probability that such deviations as are observed may be due to chance is approximately 0.88, which means that only about once in eight trials would as good a fit be expected. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VIa, b, c	
Observed.....	847	282	281	94	267	233	2,004
Calculated....	845	282	282	94	282	219	2,004
Difference....	+2	0	—1	0	—15	+14	0

Backcrosses with green VIc.— In addition to the F_2 results noted above as derived from self-pollinated F_1 purple plants, a few F_1 purples were back-

crossed with the triple recessive green, type VIc. The records of these crosses, seven in all, are presented in table 6. The results are, as expected, in close agreement with the backcross data from the cross of purple with green. The comparison below indicates a good fit of calculated to observed frequencies for the lot as a whole. The probability that such deviations as are observed may be due to mere chance is about 0.82, indicating that as great departures from expectation as these might be expected about four times in five trials. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VIa, b, c	
Observed.....	84	72	78	72	79	249	634
Calculated....	79	79	79	79	79	237	632
Difference....	+5	—7	—1	—7	0	+12	+2

Backcrosses of Ia x VIc and IVa x V with IVa

Purple plants of F_1 of the crosses purple x green and dilute sun red x brown were crossed with homozygous dilute sun red stocks. On the basis of the hypothesis used above, the F_1 plants are assumed to be *A a B b Pl pl* and the dilute sun red plants *A A b b pl pl*. Four classes of plants, purple, sun red, dilute purple, and dilute sun red, should be produced in equal numbers by this cross. The data are presented in table 7 (page 125). Progenies of F_1 plants from the cross purple x green are listed in group 1 and those from the cross dilute sun red x brown in group 2. As will be seen from the comparison below, the observed numbers are in fair agreement with the hypothesis. The probability that such deviations as occur may be due to chance is approximately 0.67. In other words, there are two chances in three that deviations of this sort are due to errors of random sampling alone. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed.....	299	270	288	291	1,148
Calculated.....	287	287	287	287	1,148
Difference.....	+12	—17	+1	+4	0

Behavior of F_2 color types in later generations

From all the foregoing it appears that the results obtained are in close accord with the proposed three-factor hypothesis in the case of both the cross purple x green and the cross dilute sun red x brown, and not alone for the F_1 and F_2 generations but also for backcrosses with green and with dilute sun red. It is now in order to inquire into the behavior of these crosses in F_3 and later generations. In the presentation of the additional data, the two crosses purple x green and dilute sun red x brown will be considered together.

Later behavior of F_2 purple Ia.— Purple plants of the F_2 generation of the crosses under consideration are expected to be of eight genotypes. The expected F_2 genetic formulae and the F_3 color classes, together with the relative numbers of each, are as follows:

F_2 genotypes	F_3 color types					
	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VI
1 — *A A B B Pl Pl*	1	.....	.....	.....	.....	.....
2 — *A A B B Pl pl*	3	1	.....	.....	.....	.....
2 — *A A B b Pl Pl*	3	.....	1	.....	.....	.....
2 — *A a B B Pl Pl*	3	.....	.....	.....	1	.....
4 — *A A B b Pl pl*	9	3	3	1	.....	.....
4 — *A a B B Pl pl*	9	3	.....	.....	3	1
4 — *A a B b Pl Pl*	9	.....	3	.....	3	1
8 — *A a B b Pl pl*	27	9	9	3	9	7

If, instead of being selfed, the F_2 purple plants are backcrossed to green of type VIc, the same F_3 color classes are expected but the several classes should, of course, be equally frequent except in case of the F_2 triple heterozygotes, which should throw three times as many greens as of each of the other five types.

The F_3 data from thirty-five F_2 plants are recorded in table 8 (page 125). In group 1 of the table are listed the progenies of eight selfed and one backcrossed F_2 plants. From the backcross six color types appeared in frequencies of 4:4:11:4:4:18. The theoretical number for the first

five classes is 5.6 and for the sixth class is 17. The probability that such deviations as occur are due to chance is approximately 0.35, or more than one in three. The eight self-pollinated plants gave together the six types in frequencies as follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VIa, b, c	
Observed.....	193	66	60	16	57	34	426
Calculated.....	180	60	60	20	60	46	426
Difference.....	+13	+6	0	—4	—3	—12	0

The probability that such deviations as occur may be due to errors of random sampling is practically 0.27. Similar deviations might therefore be expected somewhat more than once in four trials. It will be noted that two progenies lacking class IV are included in this lot (group 1, table 8). The total number of plants in these progenies were 37 and 17, respectively, and they should therefore have had, respectively, two and one plants in class IV.

Five F_2 purple plants (group 2, table 8) gave four color types (Ia, IIa, IIIa, and IVa) in F_3, with total frequencies as shown below. Here the probability, P, equals 0.75, indicating that deviations of this magnitude might be expected thru chance in three out of four trials. The comparison of observed with theoretical distributions follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed.....	102	36	29	13	180
Calculated.....	101	34	34	11	180
Difference.....	+1	+2	—5	+2	0

Progenies of seven other purple F_2 plants (group 3, table 8) consisted of the four color types Ia, IIa, V, and VIa. Four of these F_2 plants were self-pollinated and gave a total of 164 F_3 plants. Four, including one that was also selfed, were backcrossed to green and yielded a total of 209 F_3 plants. For the progenies from selfed F_2 plants $P = 0.20$, and for those from backcrossed plants $P = 0.57$. There is, therefore, one chance in five

in the one case and considerably more than an even chance in the other case that deviations of the kind noted may have been due to errors of random sampling. The comparisons follow:

	Color types	Purple Ia	Sun red IIa	Brown V	Green VIa	Total
Selfed	Observed	95	31	23	15	164
	Calculated	92	31	31	10	164
	Difference	+3	0	—8	+5	0
Backcrossed	Observed	54	58	44	53	209
	Calculated	52	52	52	52	208
	Difference	+2	+6	—8	+1	+1

Seven self-pollinated F_2 purple plants gave progenies consisting of the four color types Ia, IIIa, V, and VIb (group 4, table 8). Here $P=0.75$, indicating that there are three chances in four that such deviations as are shown are due to chance. The comparison follows:

Color types	Purple Ia	Dilute purple IIIa	Brown V	Green VIb	Total
Observed	318	114	111	42	585
Calculated	329	110	110	37	586
Difference	—11	+4	+1	+5	—1

Five F_2 purple plants from self-pollination gave only two color types (Ia and IIa) in F_3 (group 5, table 8). The total number of F_3 individuals was 183, of which 139 were of color type Ia and 44 were of color type IIa, the expected numbers being, respectively, 137 and 46, and the deviation equaling 2 ± 4. One of these F_2 plants was also backcrossed to two greens, resulting in 12 purple and 9 sun red F_3 plants where equality of the two classes was expected. The deviation here is 1.5 ± 1.5.

Finally, two self-pollinated F_2 purple plants produced 217 F_3 individuals (group 6, table 8) of color types Ia and IIIa. There were 168 purple

and 49 dilute purple where the expected numbers were 163 and 54, respectively — a deviation of 5 ± 4.3.

It is seen, then, that in every case the F_3 progenies of F_2 purple plants were of color types expected on the basis of the three-factor hypothesis, and that the F_3 distributions within any group were in close agreement with expectation. It is particularly noteworthy, however, that not all types of F_3 behavior were observed, and that the distribution of the progenies of the thirty-five F_2 plants tested was in rather imperfect agreement with expectation. Thus, no F_2 purple plant bred true in F_3 where one such plant was expected, and none gave progenies of purple and brown only where at least two with such behavior were expected. It has already been pointed out (page 35) that eight classes of behavior of F_2 purples are looked for, and that any twenty-seven F_2 purple plants should be distributed with respect to their F_3 behavior in the relation 1:2:2:2:4:4:4:8. The actual and theoretical distributions are compared as follows:

Observed.....	0	5	2	0	5	7	7	9	35
Calculated.....	1.3	2.6	2.6	2.6	5.2	5.2	5.2	10.4	35.1
Difference.....	−1.3	+2.4	−0.6	−2.6	−0.2	+1.8	+1.8	−1.4	−0.1

While mere inspection of the above comparison might suggest poor agreement between theory and observation, nevertheless $P = 0.36$, indicating that such deviations as occur might be expected in more than one out of three trials, which is not a bad fit. So far, therefore, the available data are in fair accord with the three-factor hypothesis.

Before taking up a consideration of the F_3 behavior of other F_2 color types, it will be well to consider briefly the F_4 behavior of F_3 purple plants. Only one F_3 purple of the lot having all six color types (table 8, group 1), comparable to F_2 purples, was tested in F_4. This one plant gave an F_4 with the four color types Ia, IIa, V, and VIa.

Only eight other F_3 purple plants were tested in F_4. All these belonged to the lot consisting of color types Ia, IIIa, V, and VIb (group 4, table 8). The F_2 purple plants giving rise to this group are assumed to have been of the genotype *A a B b Pl Pl*. The F_3 purple plants should therefore have been of four genotypes and should have given F_4 behavior as follows:

F_3 genotypes	F_4 color types			
	Purple Ia	Dilute purple IIIa	Brown V	Green VIb
1—*A A B B Pl Pl*	1	.....	.....	.....
2—*A A B b Pl Pl*	3	1	.....	.....
2—*A a B B Pl Pl*	3	.....	1	.....
4—*A a B b Pl Pl*	9	3	3	1

The data are presented in table 9. Four F_4 progenies (group 1) were made up of the four color types Ia, IIIa, V, and VIb. The total numbers of plants of each of the four types, as seen below, were in close accord with expectation, P equaling 0.57. There is more than an even chance that such deviations as those observed may have been due to errors of random sampling. The comparison of observed with calculated results follows:

Color types	Purple Ia	Dilute purple IIIa	Brown V	Green VIb	Total
Observed	185	68	74	20	347
Calculated	195	65	65	22	347
Difference	—10	+3	+9	—2	0

Three of the eight purple F_3's (group 2) gave in F_4 only purple and dilute purple plants, 88 of the former and 28 of the latter. The expected numbers were 87 and 29, respectively, showing a deviation of 1 ± 3.1.

One of the eight F_3 purples (group 3) gave 67 purple and 21 brown plants in F_4, while the expected numbers were 66 and 22, respectively. The deviation here is only 1 ± 2.7.

None of the eight F_3 purples bred true, but only one in nine was expected to do so. As already indicated, the theoretical distribution of nine F_3 purples of the sort here under consideration, with respect to the four kinds of behavior in F_4, is 1:2:2:4. The observed distribution was 0:3:1:4. There is more than an even chance that these deviations may have been due to errors of random sampling, P equaling 0.57.

It should not be forgotten that, while a very poor fit of observation to hypothesis, as measured by values of P, throws doubt upon the correctness of the hypothesis, it does not follow that a good fit proves the hypothesis to be true. This is particularly true where small numbers are dealt with. It will be recalled in this connection that, owing probably to the small numbers tested, no F_2 purple has been found to breed true in F_3 and none has been found to give only purple and brown offspring. It has been shown, however, that purple plants of the genotype *A a B B Pl Pl* exist, since one F_3 purple threw only purple and brown plants in F_4. Moreover, one of these F_4 purples repeated this behavior in F_5. Similarly it can be said that purples of the genotype *A A B B Pl Pl* have been recovered from the crosses under consideration, for two F_4 purple plants of the lot composed of purples and dilute purples (group 2, table 9), when backcrossed to green, gave 18 purple plants and no other types in the next generation, and one of these two F_4 purples, when crossed back to dilute sun red, gave 34 purple plants. Two other purples of the same F_4 lot, when similarly crossed, gave both purple and dilute purple, 23 of the former and 18 of the latter. Purple plants of all the expected genotypes have therefore been recovered in one or another generation from F_2 to F_4 from the original crosses of purple x green and dilute sun red x brown. Moreover, these genotypes have been found in numbers not far from what might reasonably be expected considering the relatively small numbers tested. It now remains to inquire into the F_3 and later behavior of F_2 color types other than purple.

Later behavior of F_2 sun red IIa.— Sun red plants of F_2 of the crosses purple x green and dilute sun red x brown are expected, in accordance with the three-factor hypothesis, to be of four sorts with respect to their behavior in F_3, as follows:

F_2 genotypes	F_3 color types		
	Sun red IIa	Dilute sun red IVa	Green VIa, c
1 — *A A B B pl pl*	1	.....	.....
2 — *A A B b pl pl*	3	1	.....
2 — *A a B B pl pl*	3	.....	1
4 — *A a B b pl pl*	9	3	4

Only nine F_2 sun red plants were tested by their F_3 behavior, and no later generations were grown. All the available data are given in table 10 (page 128). Five F_2 plants, when self-pollinated (group 1 of the table), gave the expected three classes of progeny, sun red, dilute sun red, and green, with a distribution of the F_3 plants as given below, and in addition a single brown plant. To include this unexpected plant in the comparison with the calculated distribution would give zero as the value of P, which is equivalent to saying that even in an infinite number of trials there is no chance of finding such a plant thru errors of random sampling. The single off-type plant is readily accounted for by supposing that a grain of foreign pollen was accidentally admitted in the pollination of the parent plant. Tho it is realized that, with such a convenient supposition always at hand, almost any result can be made to fit a theory, the reality of just such accidental pollinations will not be questioned by any one who has had experience in the technique of maize pollination. With the elimination of this one plant, the fit of observation to hypothesis is almost perfect. The comparison follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed	126	42	55	223
Calculated	125	42	56	223
Difference	+1	0	—1	0

Three F_2 sun red plants, including one of the five in the former test, were crossed back to green (group 1, table 10). The same three color types were observed as in the self-pollinated plants, with the addition again of a single off-type plant, this time a purple one. Even if this plant is left out of consideration as due to an accidental pollination, the fit of observed with calculated numbers is not very good. Such deviations from theoretical behavior are to be expected thru chance alone only once in eight trials, P equaling 0.12. The comparison follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed	14	18	50	82
Calculated	20.5	20.5	41	82
Difference	—6.5	—2.5	+9	0

A single F_2 sun red plant (group 2, table 10) gave, from self-pollination, 23 sun red and 9 dilute sun red F_3 plants, a deviation from expectation of 1 ± 1.7.

A single F_2 sun red plant (group 3, table 10), when crossed with green VIc, gave 50 sun reds and 43 greens where equality was expected, a deviation of 3.5 ± 3.3.

By way of summary of the behavior of F_2 sun red plants, it must be noted that, while four sorts of behavior were expected, only three sorts were observed. While any nine such F_2 plants should be distributed with respect to the four kinds of behavior in the relation 1:2:2:4, the observed relation was 0:1:1:7. While mathematically this is not a very bad fit considering the small numbers involved, P equaling 0.24, it is inadequate for a determination of the possible genotypes of F_2 sun red plants. Fortunately, certain crosses considered later (page 51) involving the sun red type, with presumably the same genetic constitutions as the F_2 sun reds of this cross, afford a more nearly adequate test of the matter.

Later behavior of F_2 dilute purple IIIa.— F_2 dilute purple plants should present the same types of behavior in F_3 as F_2 sun reds, but, of course, with somewhat different color types appearing, as follows:

F_2 genotypes	F_3 color types		
	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c
1 — *A A b b Pl Pl*	1	.....	.....
2 — *A A b b Pl pl*	3	1	.....
2 — *A a b b Pl Pl*	3	.....	1
4 — *A a b b Pl pl*	9	3	4

The available data from this test are given in table 11 (page 129). Four F_2 dilute purples (group 1) yielded the three color types expected, dilute purple, dilute sun red, and green, in the numbers shown below. There is considerably more than an even chance that the deviations from expectation may be due to errors of random sampling, P equaling 0.58. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c	Total
Observed	95	31	50	176
Calculated	99	33	44	176
Difference	—4	—2	+6	0

One of the dilute purple F_2 plants used in this test was backcrossed with green VIc (group 1, table 11), with the result shown below. There is practically an even chance that the observed deviations may be due to errors of random sampling, P equaling 0.49. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c	Total
Observed	21	25	57	103
Calculated	26	26	52	104
Difference	—5	—1	+5	—1

One F_2 dilute purple gave 57 dilute purple and 21 dilute sun red plants in F_3 (group 2, table 11). The expected numbers were 58.5 and 19.5, respectively, the deviation being 1.5 ± 2.6.

Three F_2 dilute purples gave a total of 85 dilute purple and 20 green plants (group 3, table 11), the theoretical numbers being 79 and 26, respectively. The deviation from expectation, 6 plants, is just twice the probable error.

One F_2 dilute purple bred true in F_3, producing 21 dilute purple plants and no other types (group 4, table 11). Thus, all the sorts of behavior expected of F_2 dilute purples were realized in F_3. The distribution of the F_2 plants with respect to the four sorts of behavior was 1:1:3:4, instead of the theoretical distribution 1:2:2:4. Differences of this sort might be expected thru chance in four out of five trials, P equaling 0.80.

Only three plants of these lots were tested in F_4. One was a dilute sun red of the lot made up of dilute purples and dilute sun reds, and this one bred true in F_4 as was expected of it, producing 34 dilute sun red plants. The other two plants tested further were dilute purples of the lot containing the three color types III, IV, and VI. Both again gave these three

types, the total numbers of the respective classes being 29, 5, and 18. The expected numbers, 29, 10, and 13, show a deviation from expectation which might result thru chance about once in nine trials, P equaling 0.11.

Later behavior of F_2 dilute sun red IVa.— Dilute sun red plants of F_2 should be of two sorts, *A A b b pl pl* and *A a b b pl pl*. Five such plants were tested, with results as shown in table 12 (page 129). Of these five, two bred true, producing a total of 92 dilute sun red plants (group 2). One of these two, when backcrossed with green, gave 69 dilute sun red plants. Three of the five F_2's gave in F_3 dilute sun reds and greens, 62 of the former and 17 of the latter (group 1). The theoretical numbers were 59 and 20, respectively. The deviation of 3 plants is only a little greater than the probable error, $\pm$ 2.6. With two of the F_2 dilute sun red plants breeding true and three again throwing segregates, expectation was very nearly realized.

Later behavior of F_2 brown V.— Brown plants of F_2 are expected to be of four genotypes and to show consequent differences in behavior in F_3 as follows:

F_2 genotypes	F_3 color types	
	Brown V	Green VI
1 — *a a B B Pl Pl*	1	.....
2 — *a a B B Pl pl*	3	1
2 — *a a B b Pl Pl*	3	1
4 — *a a B b Pl pl*	9	7

Data for F_3 from fourteen F_2 brown plants are presented in table 13 (page 130). Five self-pollinated F_2 browns (group 1) gave, in addition to one sun red presumably due to accidental pollination, 96 browns and 74 greens in F_3, which is almost exactly a 9:7 relation, the deviation being 0.4 $\pm$ 4.4. Nine other selfed F_2 browns (group 2) gave in F_3 a total of 354 brown and 104 green plants. An exact 3:1 ratio for the total of 458 would be 343.5 and 114.5, respectively, the deviation being 10.5 $\pm$ 6.3. Such a deviation might be expected thru chance alone about once in four

trials. One of the F_2 brown plants that, when selfed, gave a 3:1 ratio in F_3, when crossed with green gave 34 brown and 41 green plants where equal numbers were expected, the deviation being 3.5 ± 2.9. None of the fourteen F_2 brown plants bred true in F_3. The fourteen plants should theoretically have given F_3 ratios of 1:0, 3:1, and 9:7 in approximately the respective numbers of 1.6, 6.2, 6.2, while the observed numbers were 0, 9, 5. Such deviations might occur by chance once in five trials, P equaling 0.22.

It is often difficult and sometimes practically impossible from ordinary F_3 progenies to distinguish between the two genotypes of brown which throw 3:1 progenies, namely, *a a B B Pl pl* and *a a B b Pl Pl*. The green plants thrown by the former often show some brown pigment in the exposed parts of the sheaths and husks (type VIa), a condition not seen in the greens (VIb) thrown by the latter. In some lots the brown pigment is fairly conspicuous but in others it is very weak or is absent. Again, the greens of type VIb thrown by browns of the genotype *a a B b Pl Pl* show considerable brown in the glumes of the staminate flowers. This is particularly pronounced when r^{ch} (a gene for cherry pericarp which is effective only in the presence of *Pl*) is present, but when this factor is lacking the brown color is often so faint that it is impossible to distinguish between a green plant carrying *Pl* and one lacking it. If r^{ch} is present, the green plants carrying *Pl* develop a light brownish pericarp at maturity while those lacking *Pl* never show this pericarp color whether or not *B* is present. Here again, however, the light brownish pericarp due to r^{ch}, *Pl*, and *a a* may be wholly masked if there happens to be present another pericarp color gene, *P*, which with *a a* brings about a strong brown color of the pericarp whether or not *Pl* or *B* is present.[4] On the whole, therefore, it is difficult, and often impossible, to determine the genotype to which a brown plant belongs, by an inspection of the green plants occurring in its progeny. Because of this, the 3:1 lots of F_3 progenies of F_2 brown plants are lumped together in group 2 of table 13 without any attempt to separate them into the two classes expected. Fortunately, it is readily possible to distinguish between brown plants of the two genotypes under consideration here by means of appropriate crosses.

[4] An account of these pericarp-color factors is to be published later by Dr. E. G. Anderson, who is making a study of the pericarp colors of maize.

When brown plants of all the genotypes expected in F_2 of the crosses of purple x green or dilute sun red x brown are crossed with homozygous dilute sun red plants, the following behavior is expected in the next generation:

F_2 genotypes	F_2 x *A A b b pl pl*			
	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1 — *a a B B Pl Pl*	1	.....	.....	.....
2 — *a a B B Pl pl*	1	1	.....	.....
2 — *a a B b Pl Pl*	1	.....	1	.....
4 — *a a B b Pl pl*	1	1	1	1

A few such tests of F_2 brown plants are recorded in table 14. Two plants (group 1), on being crossed with dilute sun reds, gave purples and sun reds only, 38 of the former to 45 of the latter, where equality was expected, the deviation being 3.5 ± 3.1. One of these plants has progeny from self-pollination listed in table 13, in group 2, the 3:1 lot. This plant was expected, of course, to throw only two color types from the cross with dilute sun reds, for otherwise it should not have given a 3:1 progeny on being selfed. The two brown plants in group 1 of table 14 must have been *a a B B Pl pl*. Two other F_2 brown plants (group 2) gave 32 purple and 38 dilute purple instead of the equal numbers expected, the deviation being 3.0 ± 2.8. These plants are assumed to have been *a a B b Pl Pl*. A single F_2 brown plant (group 3) when crossed with dilute sun red gave 15 purple plants, and is therefore assumed to have been *a a B B Pl Pl*.

The behavior of several F_3 brown plants when crossed with dilute sun reds is also shown in table 14. Three of these plants were from 9:7 F_3 lots and therefore are presumably comparable with F_2 browns. One of these three (group 4) gave the four color types I to IV in the numbers 1:2:6:3. It was probably *a a B b Pl pl* and should have given a 9:7 progeny if it had been selfed. The other two F_3 browns of the 9:7 lot gave 49 purple plants (group 7) and are consequently regarded as *a a B B Pl Pl*. All the other F_3 brown plants tested were from the

3:1 lot listed in table 13, group 2. None of these should give more than two types when crossed with dilute sun red. One gave 46 purple and 1 dilute sun red (group 7), the latter doubtless from an accidental pollination of the dilute sun red mother plant. Two F_3 browns gave 22 purple and 24 sun red plants (group 5), and four produced 73 purple and 85 dilute purple plants (group 6).

To summarize, all the theoretically possible genotypes of brown plants have been found either in F_2 or in such F_3 lots as showed a 9:7 ratio of brown to green. Since these F_3's are comparable with F_2 browns, they may be added to the F_2's in this summary. Of the twenty-one brown plants thus grouped, the numbers found to belong to each genotype are compared below with the calculated numbers. The deviations are such as might be expected to occur once in three trials, P equaling 0.34. The comparison follows:

	a a B B Pl Pl	*a a B B Pl pl* or *a a B b Pl Pl*	*a a B b Pl pl*	Total
Observed.....	3	12	6	21
Calculated.....	2.3(+)	9.3(+)	9.3(+)	21
Difference.....	+0.7(−)	+2.7(−)	−3.3(+)	0

Later behavior of F_2 green VI.— All F_2 green plants should breed true phenotypically in F_3. Data from eight such F_3 progenies are given in table 15, group 1 (page 132). There were observed a total of 179 green plants, and no other types. Progenies of sixteen green plants of the F_2 lots listed in tables 3 and 6 (pages 122 and 124), produced by backcrossing F_1 purples to greens, are given in table 15, groups 2 to 5. The total number of green plants in these progenies is 311. A single brown plant found in one of these progenies is assumed to have been due to accidental pollination. Green plants are therefore found to breed true green as expected, but there is nothing in this fact to indicate that green plants of the crosses under consideration are genotypically alike. That the five genotypes expected on the basis of the three-factor hypothesis were present among the progenies listed in table 15 is demonstrated in the next section of this paper.

Intercrosses of F_2 color types

It has been shown in the preceding pages that all the six color types occurring in F_2 of a cross between purple and green behave in F_3 and later generations as is expected on the basis of the three-factor hypothesis suggested to account for the F_2 results. It remains to determine whether the several color types behave in accordance with the hypothesis when intercrossed one with another. Of the fifteen possible intercrosses between phenotypically different types, two have already been discussed. The cross of purple with green has formed the basis of the whole discussion. The cross of dilute sun red with brown, since it was expected to give the same results as the original cross of purple with green, was most conveniently considered with that cross in generations later than F_2. The results of this second cross have been in accord with expectation. The other thirteen intercrosses are now to be considered, together with intercrosses of some types that are phenotypically alike.

Dilute sun red IVa x green VIa, VIb, VIc.— The progenies of self-pollinated green plants were listed in table 15 in several groups in accordance with what was learned of their genotypic constitution by the crosses to be considered here. The regular F_3 lots, from self-pollinated F_2 greens of self-pollinated F_1 purples, were put in group 1 of table 15. Only one of the same F_2 greens (table 16, group 2) was crossed with homozygous dilute sun red, *A A b b pl pl*. The result was 67 dilute purple plants. Another green plant, an F_3 from a self-pollinated F_2 green, gave, when similarly crossed, 9 dilute purple plants (group 2). Evidently both these green plants were *a a b b Pl Pl*. Four other F_3 green plants, when crossed with dilute sun red, gave a total of 148 sun red plants (group 1, table 16). One of these four belonged to an F_3 lot containing browns and greens in a 3:1 relation, and could not, theoretically, have done other than give all sun red or all dilute purple when crossed with dilute sun red. Two of the four were from greens of an F_3 lot made up of purples, sun reds, browns, and greens, and were therefore assumed to be *a a B B pl pl*, as the crosses with dilute sun red showed them to be. One of the four green plants, however, belonged to an F_3 lot of browns and greens in a 9:7 relation and was consequently comparable to an F_2 green. A sixth F_3 green also belonged to a 9:7 lot, comparable to an F_2 lot. When crossed with dilute sun red (group 3, table 16), it gave 24 dilute sun red plants,

and is therefore assumed to have been *a a b b pl pl*. All three of the theoretically possible homozygous genotypes have therefore been demonstrated among the F_2 greens or among F_3's comparable to F_2's.

In addition to the green plants of the direct F_2 and F_3 generations, noted above, fifteen other greens were crossed with dilute sun red. All these greens belonged to a single progeny, 2019, which was the result of a backcross of an F_1 purple with a green, *a a b b pl pl* (table 3, group 1). All of them should therefore have been heterozygous for *B* or *Pl*, or have lacked these dominant genes. Seven of the fifteen, when crossed with dilute sun red, gave 110 sun red and 85 dilute sun red plants (group 4, table 16), a deviation from equality of 12.5 ± 4.7. The green parent plants are consequently regarded as *a a B b pl pl*. Five others of the fifteen green plants (group 5) gave a total of 56 dilute purple and 65 dilute sun red, a deviation from equality of 4.5 ± 3.7, and hence are assumed to have been *a a b b Pl pl*. Three of the fifteen (group 6) gave a total of 106 dilute sun red plants. These three must, it is supposed, have been *a a b b pl pl*.

Naturally, in the course of the writer's maize studies, many other crosses between green and dilute sun red have been observed. But no purpose can be served by presenting here all this mass of data. Much of it has accumulated in connection with a study of the interrelations of plant and aleurone color, and will find its appropriate place in a later publication on that topic. A few F_2 and backcross progenies of dilute sun red F_1's of such crosses are, however, listed in table 17 (page 134), to serve as an indication of the behavior of all. Three F_2 progenies (group 1, table 17) contained 269 dilute sun reds and 99 greens, a deviation from the expected 3:1 ratio of 7 ± 5.6. Five progenies of F_1 dilute sun reds backcrossed to green VIc (group 2) included 357 dilute sun reds and 358 greens, a deviation from the expected 1:1 ratio of only 0.5 ± 9.0.

The behavior of a number of the sun red and dilute purple plants listed in table 16 has been studied in F_2 and later generations. Consideration of this later behavior is conveniently deferred to a later section of this paper (pages 51 and 53), where it is taken up with other crosses which should theoretically give similar results.

Green x green, VIa, VIb, VIc.— A number of green plants of progeny 2019, discussed above, were intercrossed. That these green plants bred true green when selfed was shown by the records of table 15 (groups 3

to 5). That they were of three distinct genotypes was shown by the data recorded in table 16 (groups 4 to 6). The behavior of random intercrosses of the same green plants is now to be considered. The data are given in table 18.

The green plants that served as parents of the crosses listed in group 6 of table 16, it was decided, must have been *a a b b pl pl*. When such plants are crossed with green plants of any of the other genotypes, nothing but green plants should result. A single cross of one of these greens with a green of the constitution *a a B b pl pl* (table 16, group 4) gave 23 green plants (table 18, group 1) as expected. Another cross of one of these greens with a green of the genotype *a a b b Pl pl* (table 16, group 5) gave 22 green plants (table 18, group 2). Crosses of green plants belonging to like genotypes should, of course, give only green plants. Three crosses of plants shown to be *a a B b pl pl* (table 16, group 4) gave 72 green plants (table 18, group 3). A single cross between plants shown to be *a a b b Pl pl* (table 16, group 5) gave 24 green plants (table 18, group 4). Five crosses of plants of genotype *a a B b pl pl* with plants of genotype *a a b b Pl pl* gave a total of 40 brown and 105 green plants (table 18, group 5). Here a 1:3 ratio of brown to green is to be expected. The theoretical numbers are therefore 36 and 109, respectively, and the deviation is 4.0 ± 3.5. The important fact here is that all these intercrosses of greens gave the color types expected on the basis of the results of crosses of the same individual green plants with dilute sun reds. The writer deems himself fortunate in having been able to obtain results approximating so closely a complete demonstration of the several genotypes of green, since the selfing, the crossing with dilute sun reds, and the intercrossing of greens, were made at the same time, with the green plants chosen wholly at random.

Brown V x green VIc.— When brown plants are crossed with green plants of type VIc, the F_1 plants are brown, and browns and greens alone appear in F_2. Since brown is supposed to be *a B Pl* and type VIc green *a b pl*, the F_2 progenies should exhibit 9:7 ratios. Eleven F_2 progenies are listed in table 19 (page 135), with a total of 317 brown and 223 green plants. The theoretical numbers are 304 and 236, respectively, showing a deviation of 13 ± 7.8. There is more than one chance in four that such a deviation is due to errors of random sampling, P equaling 0.27.

Of any nine F_2 brown plants of this cross, theoretically one should breed true in F_3, four should give a 3:1 ratio, and four should give a 9:7 ratio. Six F_2's were tested, with the results shown in table 20. Two bred true, with a total of 29 brown plants (group 1). Two gave ratios classed as 3:1, the totals (group 2) being 100 brown to 40 green, a deviation of 5.0 ± 3.5. Two gave progenies interpreted as 9:7 (group 3), totaling 39 brown and 39 green, the deviation being 5.0 ± 3.0. Of the 3:1 F_3 lot, two browns bred true in F_4, producing 59 brown plants, and one green bred true, producing 56 green plants.

The distribution of the F_2 brown plants with respect to their F_3 behavior — two breeding true, two throwing a 3:1 ratio, and two a 9:7 ratio — was as near expectation, 1:4:4 in nine, as could perhaps be expected from such small numbers. If these six F_2 browns are combined with the fourteen F_2 browns of the original cross of purple x green noted earlier in this paper (page 44), a very good fit of the hypothesis and observation is found ($\chi^2 = 0.88$). Theoretically these two lots of F_2 browns should be of the same genotypes, so that they may well be so combined. The comparison follows:

F_3 ratios	1:0	3:1	9:7	Total
Observed	2	11	7	20
Calculated	2	9	9	20
Difference	0	+2	−2	0

Sun red IIa x green VIc.— When both parents are homozygous, the cross of green of type VIc with sun red results in sun red plants only. Three such crosses gave 112 sun red plants. Crosses with heterozygous sun red plants gave F_1 progenies of sun red together with dilute sun red or green or both, depending presumably upon whether one or the other or both of the factors *A* and *B* were heterozygous. F_1 sun red plants of such crosses are presumed to have the formula *A a B b pl pl*, and should therefore produce in F_2 the three color types sun red, dilute sun red, and green, in the relation 9:3:4. Sixteen F_2 progenies of such crosses are listed in table 21, group 1 (page 136). It has already been shown (page 48) that crosses of some green plants, *a B pl*, with dilute sun reds, *A b pl*, give sun red F_1 offspring, which are also assumed to be *A a B b pl pl*. Five F_2 progenies of such crosses are, for convenience, considered here

(group 2, table 21) with the crosses of sun red and green. While certain of the individual progenies, due perhaps to the small numbers concerned, deviate considerably from the expected results, the twenty-one progenies (groups 1 and 2, table 21) taken together approach so closely to expectation that there is more than one chance in four that the observed deviations may be due to errors of random sampling, P equaling 0.28. The comparison of observed with expected numbers follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed:				
IIa x VIc	827	268	383	1,478
IVa x VIa	343	120	179	642
Total	1,170	388	562	2,120
Calculated	1,193	398	530	2,121
Difference	—23	—10	+32	—1

F_1 sun red plants, *A a B b pl pl*, were also backcrossed with green plants of type VIc, *a b pl*. Fifteen progenies of these backcrosses are listed in table 21, the progenies from the cross IIa x VIc in group 3 and those from the cross IVa x VIa in group 4. The expected relation of 1:1:2 was realized fairly well in the results, the odds against the observed deviations' being due to chance being about three to two, P equaling 0.39. The observed and expected results are compared as follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed:				
(IIa x VIc) x VIc	134	123	267	524
(IVa x VIa) x VIc	442	465	962	1,869
Total	576	588	1,229	2,393
Calculated	598	598	1,196	2,392
Difference	—22	—10	+33	+1

Dilute purple IIIa x green VIc.— Since dilute purple differs from sun red merely in having the dominant *Pl* factor instead of *B*, crosses of dilute purple with green of type VIc should behave just as did the crosses considered in the preceding section, except that dilute purples take the place of sun reds in the progeny. Eight crosses of dilute purple with green of type VIc resulted in 91 dilute purple plants. The F_2 results of these crosses are given in table 22, group 1. Since the F_1 plants of these crosses are assumed to have been *A a b b Pl pl*, the F_2 results should be the same as those expected from crosses of greens of type VIb with dilute sun reds. The F_1's of the latter crosses have already been discussed (page 48). The F_2 results, six progenies, are for convenience considered here (group 2, table 22). While the expectation of a 9:3:4 relation was not very closely realized in the observed results, such deviations as those found might be expected thru chance about once in eight trials, P equaling 0.13. The comparison of observed and expected distributions follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c	Total
Observed:				
IIIa x VIc	416	149	173	738
IVa x VIb	274	102	107	483
Total	690	251	280	1,221
Calculated	687	229	305	1,221
Difference	+3	+22	—25	0

A single F_1 plant backcrossed with green gave the same three color types in the relation 26:20:56. The theoretical distribution is 25.5:25.5:51.0. Deviations of the observed order might be expected somewhat more than twice in five trials, P equaling 0.44.

Seven F_2 greens bred true in F_3 with a total of 359 individuals. One dilute sun red F_2 plant bred true with a progeny of 156 dilute sun red plants. Of the F_2 dilute purples, some bred true, some threw the three types seen in F_2, some gave only dilute purple and dilute sun red, and some gave only dilute purple and green. Notwithstanding the rather poor fit in F_2, therefore, the fact that practically all the expected classes

of behavior were exhibited in F_3 makes it seem likely that the deviations in F_2 were due mainly to chance.

Sun red IIa x brown V.— A single cross of brown with sun red gave purple plants only, as was expected. Since both parents were homozygous, all the F_1 plants should have been of the genotype *A a B B Pl pl* and should have produced in F_2 the four types purple, sun red, brown, and green, in the relation 9:3:3:1. The three F_2 progenies of this cross are recorded in table 23 (page 137). The expected color types were produced in approximately the expected numbers. The odds against the observed deviations' being due to chance are three to two, P equaling 0.40. A comparison of observed with expected distributions follows:

Color types	Purple Ia	Sun red IIa	Brown V	Green VIa	Total
Observed	120	29	37	10	196
Calculated	110	37	37	12	196
Difference	+10	—8	0	—2	0

Purple Ia x brown V.— Crosses of brown with purple gave purple F_1's, and four F_2 progenies gave a total of 116 purple and 38 brown plants, which is very near the 3:1 ratio expected from F_1 plants of the genotype *A a B B Pl Pl*, the deviation being 0.5 ± 3.6. Nine F_1 purples backcrossed to browns gave progenies totaling 484 purple and 477 brown plants, a deviation from the expected equality of 3.5 ± 10.5.

Purple Ia x sun red IIa.— Purples and sun reds should differ by a single factor pair, *Pl pl*. The F_1 purples backcrossed to sun red should give a 1:1 ratio of the parental types. Five such backcrosses gave 47 purple and 57 sun red plants, a deviation from expectation of 5 ± 3.4. No progenies of selfed F_1's were observed.

Purple Ia x dilute purple IIIa.— Purples are assumed to differ from dilute purples by the factor pair *B b*. Six F_1 purples backcrossed with dilute purple gave 40 purple and 52 dilute purple plants. This is a deviation from the expected equality of 6 ± 3.2. No other tests of the cross of purple x dilute purple were made.

Sun red IIa x dilute sun red IVa.— Sun reds and dilute sun reds should differ in one factor pair, *B b*, and should therefore give a simple 3:1 result in F_2. The F_1 generation of six crosses of these color types consisted of 135 sun red plants. Sixteen F_2 progenies listed in group 1 of table 24

(page 138) totaled 998 sun red and 314 dilute sun red, a deviation from the 3:1 ratio of 14 ± 10.6.

Fourteen backcrosses of F_1 sun red plants with dilute sun reds (group 2, table 24) resulted in 811 sun reds and 742 dilute sun reds, a deviation from the expected equality of 34.5 13±.3.

Two F_2 dilute sun reds bred true in F_3 as expected (table 25, group 1), with a total of 50 dilute sun red offspring. Two F_2 sun red plants (group 2) gave a total of 19 sun reds in F_3, and a third F_2 plant, on backcrossing with dilute sun red, gave 101 sun reds. Four other F_2 sun red plants gave both sun reds and dilute sun reds in their F_3 progenies (group 3), the respective numbers being 373 and 127; the calculated numbers are 375 and 125, respectively, showing a deviation of 2 ± 6.5. Of the seven F_2 sun reds tested, four were heterozygous and three apparently homozygous for the *B* factor. On the whole, therefore, the crosses of sun red with dilute sun red behaved approximately as expected.

Dilute purple IIIa x dilute sun red IVa.— Five crosses of dilute sun red with dilute purple gave a total of 344 F_1 plants, all dilute purple. Since these F_1's are supposed to be heterozygous for the *Pl* factor only, a 3:1 F_2 distribution of color types should result. Seven F_2 progenies listed in group 1 of table 26 (page 139) had a total of 261 dilute purple and 87 dilute sun red plants, exactly a 3:1 relation. Five F_1 plants were backcrossed with dilute sun red (group 2) and resulted in 275 dilute purples and 263 dilute sun reds. The deviation from the theoretical 1:1 relation is 6 ± 7.8.

Only two F_2 dilute purples were tested by their F_3 behavior. Neither bred true, the total produced being 38 dilute purples to 17 dilute sun reds, a deviation from the 3:1 ratio of 3.3 ± 2.2. As far as they go, then, the results are in close agreement with what is expected of the crosses here under consideration.

Sun red IIa x dilute purple IIIa.— Theoretically, crosses of sun red, *A B pl*, with dilute purple, *A b Pl*, should give purple, *A B Pl*, in F_1. Two crosses, as shown in group 1 of table 27 (page 140), gave a total of 24 purple and no other types. Here the parents were doubtless homozygous. If one or the other of the parents is heterozygous two color types are to be expected in F_1. A single cross (group 2, table 27) gave 74 purple and 75 sun red plants. Such a result is to be expected when the sun red parent is homozygous, *A A B B pl pl*, and the dilute purple parent is heterozygous, *A A b b Pl pl*. Two other crosses (group 3) gave

a total of 28 purple and 29 dilute purple plants. The parents are therefore assumed to have been *A A B b pl pl* and *A A b b Pl Pl*, tho the same results should have been obtained if one or the other, but not both, of the parents had been *A a*. The important point here is that purple plants were produced in all crosses, showing that sun red and dilute purple carry complementary factors for purple. The factors are assumed, in keeping with the hypothesis under test, to be *B* and *Pl*.

In accordance with this hypothesis, the F_1 purple plants should be *A A B b Pl pl* and should throw four color types in F_2. No direct F_2 progenies have been observed, but seven progenies from backcrosses of F_1 purples with dilute sun reds are recorded in table 28. While the deviations from the expected equality among the four classes are rather large, they are not greater than might occur by chance about once in four trials, P equaling 0.26. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed	99	110	104	83	396
Calculated	99	99	99	99	396
Difference	0	+11	+5	—16	0

Purple Ia x dilute sun red IVa.— Crosses of purple with dilute sun red should give purple F_1 plants, *A A B b Pl pl*, and 9:3:3:1 F_2 progenies. Four such crosses resulted in 65 purple plants in F_1. The F_2 results are reported in table 29, group 1. The distribution of the individuals of the twenty-six progenies taken together is shown below in comparison with the calculated distribution. The four color types expected were observed in approximately the expected numbers. Deviations such as shown might be expected thru chance about twice in eleven times, P equaling 0.18.

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed	1,013	316	296	100	1,725
Calculated	970	323	323	108	1,724
Difference	+43	—7	—27	—8	+1

Some of the F_1 purple plants were crossed back to dilute sun red, with results as given in group 2 of table 29 and summarized below. The seventeen progenies together approached the expected equality of the four color types so closely that the observed deviations might be expected thru chance more than twice in five trials, P equaling 0.44.

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	323	306	325	289	1,243
Calculated	311	311	311	311	1,244
Difference	+12	—5	+14	—22	—1

Sixteen F_2 purple plants were tested by their F_3 progenies (table 30). Seven F_2 purples (group 1) gave again the four color types purple, sun red, dilute purple, and dilute sun red, the several classes being represented by 268, 105, 78, and 28 individuals, respectively, while the calculated numbers were 269, 90, 90, and 30. The odds against such deviations being due to chance are about three to one, P equaling 0.24. One of the seven F_2 purple plants was crossed with green *a a b b pl pl* and gave the same four classes of progeny, represented by 26, 25, 24, and 21 plants, respectively. Evidently these F_2 purples were like the F_1's, *A A B b Pl pl*.

Four other F_2 purples (group 2, table 30) gave only purple and sun red progenies. Three of these when selfed gave 60 purple and 22 sun red. Two of these three and one other, when backcrossed with dilute sun red or green, gave 32 purples and 31 sun reds. The four F_2's are therefore regarded as *A A B B Pl pl*.

Five F_2 purples (group 3) gave purples and dilute purples only. Four of these, which were selfed, gave 162 purples and 48 dilute purples, while the fifth, which was backcrossed to dilute sun red, gave 17 purples and 15 dilute purples. These five F_2's are consequently regarded as *A A B b Pl Pl*.

None of the sixteen F_2 purples tested bred true in F_3, *A A B B Pl Pl*. A single F_3 purple (group 6), however, which occurred in the F_3 lot showing the four color types (group 1) and which was therefore comparable to the F_2 purples, bred true in F_4, producing 69 purples on being selfed and 18 on being backcrossed to green. Of three other F_3 purples of the same

F_3 lot, two (group 4) gave only purples and sun reds, and one (group 5) gave only purples and dilute purples.

The twenty F_2 and F_3 purples tested, therefore, were distributed with respect to the four kinds of behavior in the relation 7:6:6:1, in contrast to the calculated distribution of approximately 8.9:4.4:4.4:2.2. There is more than an even chance that such a difference may be due to errors of random sampling, P equaling 0.53. On the whole, therefore, the F_2 purples of this cross behaved in later generations as was expected of them.

F_2 sun red plants of the cross purple x dilute sun red showed two types of behavior in F_3 (table 31, group 1). Three F_2's bred true, with 53 sun red plants in F_3. Four gave a total of 70 sun red and 24 dilute sun red plants. Where an expected ratio of one true breeding to two segregating progenies was expected, the observed relation of three to four is not a bad fit.

F_2 dilute purples also showed the two types of behavior expected in F_3 (group 2, table 31). Three bred true, with a total of 97 dilute purple plants, and six gave a total of 217 dilute purple and 86 dilute sun red plants. The 1:2 ratio was therefore exactly realized.

Three F_2 dilute sun reds bred true in F_3 (group 3) as was expected of them, producing a total of 72 dilute sun red plants.

Numerous F_3 plants of the several color types of the cross under consideration here were tested by F_4 and F_5 progenies, with results wholly consistent with expectation. It is deemed unnecessary to give the records of these later generations in detail.

Evidence from aleurone-color and linkage relations

The evidence presented up to this point in support of the three-factor hypothesis, involving *A a*, *B b*, *Pl pl*, has had to do with the behavior of the several F_2 color types in later generations and in intercrosses. There remain to be discussed some bits of evidence which, while less direct, are perhaps no less trustworthy. This evidence deals with (1) the relation of aleurone color to plant-color types, (2) the linkage of certain plant-color types with endosperm color, and (3) the linkage of other color types with the liguleless leaf.

Relation of aleurone color to plant color.— Of the plant-color factors considered in this section of the paper, the pair *A a* is concerned also in the development of aleurone color. It has been shown by the writer

in a previous paper (Emerson, 1918) that the presence of three dominant factors, *A*, *C*, and *R*, is necessary for the development of aleurone color. It is assumed that the factor pair *A a* for aleurone color is identical with the pair *A a* for plant color. Some of the evidence on which this assumption is based may well be considered at this point in order to justify the use of the same symbols for both plant and aleurone color. After the identity of *A a* has been established, certain relations of aleurone color to plant color can be used to check up some of the conclusions previously drawn with respect to the genetic interrelations of the several plant-color types.

It will be recalled that dilute sun red crossed with green gave dilute sun red in F_1 and a 3:1 ratio of the two types in F_2 (table 17, group 1, page 134), and that backcrosses of F_1 with green gave a 1:1 ratio (group 2). The F_2 seeds of these F_1 plants also exhibited a 3:1 relation — 424 colored and 127 colorless, deviation 10.8 ± 6.9 — thus showing that only one factor pair, *A a*, *C c*, or *R r*, was heterozygous. The colorless seeds produced 98 green plants, and the colored ones produced 269 dilute sun reds and 1 weak plant, recorded as green, which died in the seedling stage. Obviously the factor that differentiates dilute sun red from green is the same as the one that in these cases differentiated the colored from the colorless seeds, or some factor very closely linked with it. Fortunately, F_1 plants closely related to the ones which when selfed showed the behavior noted above, were backcrossed with green, colorless-seeded *A* testers (Emerson, 1918). Of the resulting seeds 632 were colored and 590 were colorless, evidently a 1:1 relation — the deviation being 21 ± 11.8 — showing that the F_1 plants were, with respect to aleurone color, *A a C C R R*. The colored seeds gave rise to 357 dilute sun red plants and the colorless seeds to 358 green plants. Evidently, therefore, it is the *A a* pair that differentiates dilute sun red from green. This is in support of the assumed genotypes *A b pl* and *a b pl* for dilute sun red and green, respectively.

The single progeny recorded in group 3 of table 9 (page 127) came from a plant known to be *A a* with respect to aleurone color and producing 130 colored and 41 colorless seeds. The 3:1 aleurone-color relation shows it to have been heterozygous in only one aleurone-color factor, and therefore *A a C C R R*. The colored seeds, *A C R*, produced 67 purple plants, and the colorless ones, *a C R*, produced 21 brown plants.

Evidently, purples are differentiated from browns by the *A a* pair alone, just as dilute sun reds are differentiated from greens. This is quite in keeping with the assumed genotypes, *A B Pl* and *a B Pl*, for purple and brown, respectively.

Two of the progenies recorded in group 3 of table 8 (page 126) involved both aleurone and plant color. The heterozygous parents were backcrossed with green *A* testers and produced 125 colored and 127 colorless seeds. The factor pair differentiating these two seed classes was therefore *A a*. The colored seeds, *A C R*, produced 15 purple and 14 sun red plants, while the colorless seeds, *a C R*, gave 9 brown and 14 green plants. Since it is shown in the preceding paragraph that purples and browns differ with respect to the pair *A a* alone, it may be inferred that the sun reds and the greens of these lots also differed with respect to *A a* alone. The assumption heretofore made with respect to the genotypes of these color classes, *A B Pl*, *A B pl*, *a B Pl*, and *a B pl*, for purple, sun red, brown, and green, respectively, is given support by this relation of aleurone color to plant color.

Two of the progenies recorded in group 1 of table 9 (page 127), and one in group 4 of table 8 (page 126), were grown from self-pollinated plants known to be *A a* with respect to aleurone color and found to have 644 colored and 228 colorless seeds. The 3:1 seed-color relation shows them to have been *A a C C R R*. The colored seeds, *A C R*, gave 294 purples and 113 dilute purples, while the colorless seeds, *a C R*, gave 119 browns and 40 greens. If purples and browns differ with respect to *A a* alone, as they have been shown to do, presumably the dilute purples and the greens of these lots also differ in the same way. This is in keeping with the assumption that the genotypes of the color classes are *A B Pl*, *A b Pl*, *a B Pl*, and *a b Pl*, for purple, dilute purple, brown, and green, respectively.

These comparisons of the relations of aleurone color to plant color have confirmed definitely the supposition that purples, sun reds, dilute purples, and dilute sun reds have the dominant factor *A*, and browns and greens the recessive factor *a*. The comparisons have also afforded some support for the assumed genetic constitution of the several color types with regard to *B b* and *Pl pl*. More definite evidence for the latter, however, is afforded by the linkage relations now to be discussed.

Linkage of plant color with endosperm color.— It has been known since 1912 that a linkage exists between the factor pair *Pl pl* and endosperm

color. The data suggest irregularities or complexities which cannot be straightened out until more definite information is at hand with regard to the two or more factor pairs concerned in the development of yellow endosperm.[5] Only such data are presented here as are necessary to show the relations of the several plant-color types to endosperm color.

A single progeny recorded in table 27, group 2 (page 140), was made up of 74 purple and 75 sun red plants. The lot resulted from a cross of a white-seeded sun red plant with a dilute purple plant which was heterozygous with respect to both yellow endosperm and plant color. The yellow seeds produced 58 purple and 20 sun red plants, and the white seeds produced 16 purple and 55 sun red plants. The yellow-seeded sun reds and the white-seeded dilute purples are known to be the crossover classes. The ratio of non-crossovers to crossovers is 113:36, and the percentage of crossing-over, therefore, is 24.2. Evidently a factor pair for yellow endosperm, *Y y*, is linked with the factor pair that differentiates purple from sun red. In accordance with the hypothesis under test, this plant-color factor pair is *Pl pl* — purple = *A B Pl*, and sun red = *A B pl*.

Two other progenies (table 26, group 1, page 139) had a total of 116 dilute purple and 42 dilute sun red plants. The selfed parent plants were heterozygous for yellow endosperm as well as for plant color. The yellow seeds gave 99 dilute purple and 17 dilute sun red plants, and the white seeds gave 17 dilute purple and 25 dilute sun red plants. This F_2 distribution, as shown below, is very close to expectation ($\chi^2 = 0.26$) on the basis of 25 per cent of crossing-over between the factor pair *Yy* and the pair that differentiates dilute purple from dilute sun red. It seems likely, therefore, that the same plant-color factors, *Pl pl*, are concerned here as in the progeny consisting of purples and sun reds. This is in keeping with the theoretical genotypes, *A b Pl* and *A b pl*, assumed for dilute purple and dilute sun red, respectively. The comparison between the observed F_2 distribution and that calculated on the basis of 25 per cent of crossing-over follows:

Observed	99	17	17	25 =	158
Calculated	102	17	17	23 =	159
Difference	−3	0	0	+2	−1

[5] This problem is being investigated by Dr. E. G. Anderson.

A single progeny (table 8, group 3, page 126) from a selfed parent heterozygous for yellow endosperm, contained purple, sun red, brown, and green plants, totaling 63, in the relation 35:15:6:7. These four color types are expected to occur in a total of 64 in the relation 36:12:12:4 from a selfed plant of the genotype *A a B B Pl pl*. The observed deviation from expectation might occur by chance once in nine trials, P equaling 0.11. Theoretically, the green plants of this lot, *a B pl*, are differentiated from the browns, *a B Pl*, by the same factor pair, *Pl pl*, that differentiates the sun reds, *A B pl*, from the purples, *A B Pl*. If this is true, the same linkage relations should exist for yellow endosperm with the brown-green lot as with the purple-sun-red lot. From yellow seeds there came 29 purples and 8 sun reds, and from white seeds 6 purples and 7 sun reds. Such a distribution should be very closely realized ($\chi^2 = 0.97$) from 30 per cent crossing-over between *Y y* and *Pl pl*. The yellow seeds produced also 5 brown and 3 green plants, and the white seeds 1 brown and 4 green plants. While the number of individuals is too small to give a reliable indication, it is of interest to note that the coefficient of association (Collins, 1912) calculated from the series 5:3:1:4, or 0.739, is practically that calculated from 26 per cent of crossing-over. In so far as these records go, therefore, they support the assumption that brown and green in this lot are differentiated by the same factor pair as are purple and sun red, and thereby support the hypothesis under test.

A plant heterozygous for the three plant-color pairs *A a*, *B b*, *Pl pl*, and for *Yy*, backcrossed with a white-seeded green plant of type VIc, *a b pl y*, gave the six color types, purple, sun red, dilute purple, dilute sun red, brown, and green, in the numerical relation 10:13:17:11:9:33 (table 6, page 124), which is a close fit (P = 0.61) to the expected relation, 1:1:1:1:1:3. From yellow seeds the resulting series was 8:6:13:2:7:17, and from white seeds it was 2:7:4:9:2:16. When the classes having *A Pl*, purple and dilute purple, were lumped together, and similarly those having *A pl*, sun red and dilute sun red, the yellow seeds gave 21 plants with *Pl* and 8 with *pl*, while the white seeds gave 6 with *Pl* and 16 with *pl*. Of these 51 plants, there were 14 in the crossover classes, or a percentage of crossing-over of about 27.5 ± 4.1, approximately the same as in the cases cited above. In this lot there are theoretically three kinds of greens, *a B pl*, *a b Pl*, and *a b pl*, one of which has *Pl* and two of which have *pl*, while all the browns, *a B Pl*, have *Pl*. If there be

assumed 25 per cent of crossing-over between *Y y* and *Pl pl*, equivalent to a 3:1:1:3 gametic series, yellow seeds should give 3 brown to 5 green, and white seeds 1 brown to 7 green, as shown below:

	Yellow	White
Brown, *a B Pl*	3	1
Green, *a B pl*	1	3
Green, *a b Pl*	3	1
Green, *a b pl*	1	3
	5	7

The yellow seeds actually gave 7 brown to 17 green and the white seeds 2 brown to 16 green, which is a close fit to the calculated relation, 3:5:1:7 (P = 0.59). In this case as in the others, then, the linkage relations between *Y y* and *Pl pl* afford additional support for the belief that the several color types actually bear to one another the relation assumed in the assignment of hypothetical genetic formulae (page 32).

Linkage of plant color with leaf type.— It has been known for some years that a leaf type termed *liguleless* (Emerson, 1912) is linked with the factor pair that differentiates sun red from dilute sun red. As an illustration of this, two backcross progenies, 8250 and 8253, with a total of 145 sun red and 147 dilute sun red plants, may be cited. These progenies came from a cross of normal-leaved sun red, *A B pl Lg*, with liguleless-leaved dilute sun red, *A b pl lg*, backcrossed with liguleless dilute sun red. Of the normal-leaved plants 104 were sun red and 41 were dilute sun red, while of the liguleless-leaved plants 48 were sun red and 99 were dilute sun red. The non-crossovers were to the crossovers as 203:89, or a percentage of crossing-over of 30.5. Since the factor pair that differentiates sun red from dilute sun red has been assigned the symbol *B b*, the linkage noted here is evidently between *B b* and *Lg lg*.

Six progenies from backcrosses of heterozygous normal-leaved purples with liguleless dilute sun reds gave purples, sun reds, dilute purples, and dilute sun reds in the relation 197:177:178:167, which is not far from the equality expected, P equaling 0.46. Among the normal-leaved plants, the four color types occurred in the relation 123:117:47:55, and among the liguleless-leaved plants in the relation 74:60:131:112. Evidently the purples bear the same relation to the dilute purples as the sun reds do to

the dilute sun reds. For sun reds and dilute sun reds, the non-crossovers are to the crossovers as 229:115, or a crossover percentage of 33.4 ± 1.7. For purples and dilute purples, the relation is 254:121, or a crossover percentage of 32.3 ± 1.5. It follows from this that the factor pair, *B b*, which differentiates sun red, *A B pl*, from dilute sun red, *A b pl*, is the same as that which differentiates purple from dilute purple. And this is in keeping with the hypothesis under test, in accordance with which purple and dilute purple have been assigned the genotypes *A B Pl* and *A b Pl*, respectively.

In a single progeny resulting from a backcross of a heterozygous normal-leaved purple plant with a liguleless-leaved green plant, greens occurred, as expected, with about three times the frequency of the average of the other five color classes. The progeny included 14 browns and 49 greens. Of the normal-leaved plants there were 10 browns and 19 greens, and of the liguleless-leaved plants 4 browns and 30 greens. On the basis of the hypothetical genotypes assigned to browns and greens, and with the assumption of 33 per cent of crossing-over between *B b* and *Lg lg*, the four classes, normal brown, normal green, liguleless brown, and liguleless green, should bear the relation 2:4:1:5. For a total of 63 plants, the relation would be approximately 11:21:5:26, whereas the observed relation was 10:19:4:30. The deviations from expectation are such as might occur by chance in more than three out of four trials, P equaling 0.78. In this case, as in the others reported, the linkage relations between *B b* and *Lg lg* afford support for the view that the several color types bear the relation to one another inferred from the hypothetical genotypes assigned them.

Summary of results involving A a, B b, Pl pl

The results of the cross of purple with green — which gave in F_2 six color types, namely, purple, sun red, dilute purple, dilute sun red, brown, and green, with a numerical relation of approximately 27:9:9:3:9:7 from selfed F_1's and about 1:1:1:1:1:3 from F_1's backcrossed to green — have been interpreted on the basis of the interaction of three factor pairs, *A a*, *B b*, and *Pl pl*. This hypothesis has been subjected to practically every genetic test available, as summarized below.

Each of the six F_2 color types has in turn been tested by its behavior in F_3, and in several cases behavior in F_4 and even in later generations

has been noted. All the possible combinations of intercrosses between the several types have been studied, except dilute purple x brown. In most cases these intercrosses have been carried to the F_2 generation, and in several instances to F_3 and F_4. Thruout the tests, the results have been in close agreement with those expected from the hypothesis. In almost every instance all the color types expected in each generation of the several crosses, and no others, have appeared. Moreover, the numerical relations found to exist between the several color types and also between the several classes of behavior have been reasonably close to expectation. It is true that in some instances the fit of observation to hypothesis has not been particularly good, but even here the observed deviations have been of such an order as might be expected to occur occasionally thru the chance errors of random sampling.

In addition to the tests afforded by the behavior of the several F_2 color types in later generations and in intercrosses, the relations of aleurone color involving the factor pair *A a* to the several plant colors, and the linkage relations of the plant-color factors *Pl pl* with the endosperm-color factors *Y y* and of the plant-color factors *B b* with the leaf-type factors *Lg lg*, have been included in the investigation. These tests have shown that the several color types bear to one another the relations to be deduced from the hypothetical genotypes assigned them.

The conclusion seems justified, therefore, that the three-factor hypothesis proposed as an interpretation of the F_2 results obtained in crosses of purple with green has been substantiated, in so far as it is possible to substantiate any hypothesis.

CROSSES INVOLVING THE MULTIPLE ALLELOMORPHS B, B^w, b^s, b

In the preceding section of this account, six color phenotypes of maize have been discussed, namely, purple, sun red, dilute purple, dilute sun red, brown, and green. In addition to these six phenotypes, green plants have been shown to consist of three genotypes, which in some instances are slightly different phenotypically. Besides these six sharply separable phenotypes, there exist certain intermediate forms. The constancy of these types from year to year, under fairly uniform environmental conditions, leaves no doubt that they are genotypically as well as phenotypically distinct from the types considered heretofore.

One of these forms, known as weak purple, type Ib, is intermediate in certain respects between purple and sun red, and in other respects between purple and dilute purple. Plants of this type, prior to the flowering stage, frequently resemble sun reds more than purples. The pigmentation of the sheaths is less intense than with purples, and in some instances less than with strong sun reds. There is, however, sooner or later a tendency for pigment to develop on the stalk beneath the sheaths (Plate V, 2). In this respect weak purples resemble dilute purples as the latter often appear in a late stage of their development. The anthers of weak purples are usually full purple, like those of purples and dilute purples, in which respect they show no resemblance to sun reds.

A second intermediate form, known as weak sun red, type IIb, stands between sun red and dilute sun red. The sheaths and husks are less extensively and less intensely pigmented than is true of full sun red, and yet exhibit much more color than in dilute sun red (Plate V, 4). The anther color of weak sun red is like that of both sun red and dilute sun red.

While the difference between the extreme sun-color types, sun red and dilute sun red, is probably only a quantitative one — as is also presumably true of the difference between purple and dilute purple — little difficulty is experienced in separating sun red from dilute sun red plants on the one hand, or purple from dilute purple plants on the other. Frequently, however, it is difficult, or even impossible, at early stages of plant growth, to separate sun reds from purples. The existence of such intermediate forms as weak purple and weak sun red adds materially to the difficulties of classification. In fact, correct classification of all these types by inspection alone is possible only at the flowering stage. For certainty in classification, even at the flowering stage, environmental conditions, particularly soil fertility, must have been favorable thruout the growing period of the plants. While infertile soil exaggerates the difference between dilute sun red and green, by bringing about an excessive development of red pigment in the one type while no color develops in the other, on fertile soil only are revealed the finer distinctions between sun red, weak sun red, and dilute sun red. It is perhaps fortunate that the genetic relations of these several types are such that ordinarily not all of them occur in a single progeny.

Interrelations of sun red IIa, weak sun red IIb, and dilute sun red IVa

Numerous crosses of weak sun reds, IIb, with dilute sun reds, IVa, have given weak sun reds in F_1 and approximately three weak sun reds to one dilute sun red in F_2, just as crosses of strong sun red with dilute sun red give three strong to one dilute sun red (table 24, group 1, page 138). Records of such crosses are given in table 32 (page 144). Twelve F_2 progenies, totaling 1729 individuals, showed the two types in the relation 1300:429, almost exactly a 3:1 ratio, the deviation being 3.3 ± 12.1. The data for F_3 of these crosses are like those for crosses of strong sun red with dilute sun red (table 25). One weak sun red F_2 bred true in F_3 with a total of 77 weak sun red offspring (table 33, group 1). Four others gave both weak and dilute sun reds (group 2), in the relation 128:54, a deviation of 8.5 ± 3.9 from a 3:1 ratio. One dilute sun red bred true (group 3), with 95 dilute sun red plants in F_3.

A cross of weak sun red, IIb, with strong sun red, IIa, gave strong sun red in F_1 and the two parent types in F_2 in the relation 71:16, a deviation from the 3:1 ratio of 5.75 ± 2.72. There is, therefore, nearly one chance in six that the observed deviation may be due to errors of random sampling, P equaling 0.16.

In none of these crosses, strong with weak, weak with dilute, and strong with dilute sun red, have other than the parent types appeared in F_2. If weak sun red is due to the action of some additional modifying factor, not heretofore considered, types other than those of the parents should have occurred in some of the crosses. The natural conclusion, therefore, is that weak sun red, IIb, is due to an allelomorph of *B* and *b*, the pair concerned with the difference between sun red, IIa, and dilute sun red, IVa. This third allelomorph, responsible for weak sun red, may well be designated B^w.

Further evidence in support of the assumption that an allelomorph of *B* and *b* is concerned with weak sun red is afforded by linkage studies involving strong, weak, and dilute sun red with leaf type. Evidence has been offered (page 63) to show that *B b* and *Lg lg* are linked with about 30 to 33 per cent of crossing-over.

A single progeny, 8252, from a sun red plant heterozygous for leaf type and plant color backcrossed to liguleless weak sun red, contained 108 sun red and 109 weak sun red plants. Of the normal-leaved plants 80

were sun red and 38 were weak sun red, while of the liguleless-leaved plants 28 were sun red and 71 were weak sun red. The ratio of non-crossovers to crossovers is 151:66, or 30.4 ± 2.1 per cent of crossing-over. The percentage of crossing-over between *Lg lg* and the factor pair differentiating sun red and weak sun red, *B* B^w, is, therefore, practically the same as the linkage between *Lg lg* and *B b*.

Four backcross progenies, 8246–8249, involving sun red, contained 469 weak sun red and 396 dilute sun red plants. Of the normal-leaved plants 153 were weak sun red and 261 were dilute sun red, while of the liguleless-leaved plants 316 were weak sun red and 135 were dilute sun red. The non-crossovers are to the crossovers as 577:288, or 33.3 ± 1.1 per cent of crossing-over. Here again, therefore, the linkage between *Lg lg* and the factor pair differentiating weak sun red from dilute sun red, B^w *b*, is practically the same as that between *Lg lg* and *B b* or between *Lg lg* and *B* B^w.

From the facts (1) that in crosses between any two of the three types sun red, weak sun red, and dilute sun red, the third type is not produced, and (2) that the linkage value between *Lg lg* and the factor pairs differentiating weak sun red from sun red and from dilute sun red is approximately the same as that between *Lg lg* and *B b*, it seems evident that weak sun red is due to a factor B^w belonging to the triple allelomorphic series *B*, B^w, *b*.

It seems probable that this series of allelomorphs contains other members in addition to the three listed above, but there is at present little conclusive evidence in support of the idea. There are certainly several forms, commonly classed as dilute sun red, that differ considerably in the amount of red pigment developed, and certainly some of these differences are genetic. As is shown in the next section of this account, some of these differences, particularly with respect to silk, anther, and leaf-blade color, are due to the effect of the aleurone-color factors *R r*. Environmental conditions, particularly soil fertility, influence the development of this pigment so greatly that the problem becomes a difficult one. There is, however, some evidence that at least two forms of dilute sun red are differentiated by a factor pair belonging to the series *B*, B^w, *b*. These forms differ principally in the amount of color in the fresh husks (Plate VI, 1 and 2), and to some extent in the sheaths, which are the plant parts most strikingly different in sun red, weak sun red, and dilute sun red.

A type of dilute sun red with stronger husk pigmentation than ordinary dilute sun red shows was crossed with an ordinary dilute purple. Leaf type also was involved in the cross. The F_1 plants were dilute purples with somewhat more pigment in the husks of young ears than is usual with that type. A single progeny, grown from an F_1 backcrossed with liguleless dilute sun red of a light type, consisted of 25 dilute purples and 18 dilute sun reds. Each of these classes was sorted with some difficulty into light and more strongly colored subclasses, in accordance with the amount of color on the husks of the young ears. Of the more strongly pigmented dilute sun reds 4 had normal and 6 had liguleless leaves, while of the lighter dilute sun reds 6 had normal and 2 had liguleless leaves. Of the more strongly colored dilute purples 4 had normal and 13 had liguleless leaves, while of the lighter ones 4 had normal and 4 had liguleless leaves. While these numbers are small and the behavior was somewhat irregular, it is perhaps noteworthy that the factor pair differentiating the lighter from the more strongly colored plants, of both the dilute sun red and the dilute purple classes, exhibited an apparent linkage with *Lg lg* of a value not far from that observed between *Lg lg* and *B b*, *B* B^w, and B^w *b*. The observed percentages of crossing-over were 32.0 for the dilute purples, 33.3 for the dilute sun reds, and 32.6 for the entire lot. This evidence, slight as it is, plainly suggests a fourth member, b^s, of the *B* series of allelomorphs, which may be stated tentatively as *B*, B^w, b^s, *b*.

Relation of weak purple Ib to purple Ia, dilute purple IIIa, and weak sun red IIb

By methods similar in the main to those outlined above, Dr. E. G. Anderson has been able to show that weak purple is differentiated from purple on the one hand and from dilute purple on the other by the same factor, B^w, that differentiates weak sun red from sun red and from dilute sun red. At the time when Dr. Anderson undertook to determine the genetic relations of weak purple, nothing was known of the relation of weak sun red to sun red and dilute sun red as presented above. Furthermore, there was no indication as to whether weak purple was differentiated from purple and dilute purple by an allelomorph of *B b* or of *Pl pl*, or by some distinct factor pair that might modify the ordinary result of the interaction of the pairs *A a*, *B b*, and *Pl pl* then known to be concerned in the production of plant colors. The evidence to be presented here

is taken almost wholly from Dr. Anderson's records, and the conclusions derived from it are his. It is with Dr. Anderson's permission and at his suggestion that, for the sake of completeness of this account of the inheritance of plant colors, his results are here presented.

A cross of a weak purple Ib with a homozygous dilute purple IIIa resulted in 25 weak purples only, while a cross of another weak purple with a homozygous dilute purple, a sib of the plant used in the first cross, gave 63 weak purples and 53 dilute purples. Two of the F_1 weak purples were backcrossed to dilute purples, and a third to dilute sun red. The result (table 34, group 1, page 145) was 141 weak purples and 163 dilute purples, a deviation of 11 ± 5.9 from equality. Five crosses of weak purples with dilute sun reds gave a total of 32 weak purples and 25 dilute purples, a deviation from equality of 3.5 ± 2.5, while two other such crosses gave 29 weak purples only. Evidently these weak purple plants differed from dilute purples by a single factor pair. This pair could not have been *Pl pl*, for the crosses of weak purple with dilute purple, *A b Pl*, gave the same results as those with dilute sun red, *A b pl*. This leaves the possibility that *B b* or some unknown factor pair was concerned.

Three crosses of weak purple Ib with purple Ia resulted in 52 purple plants. A single cross of weak purple with sun red IIa gave 18 purples. Evidently both purple and sun red carry some factor that acts to change weak purple to purple. Unfortunately, no later generations of any of these crosses were grown, but it is evident from the F_1 results and from what is known of the interrelations of purple, sun red, and dilute purple that the dominant factor *B*, common to both purple and sun red, is concerned in the change from weak purple to purple. Since the crosses of weak purple with dilute purple, *A b Pl*, and with dilute sun red, *A b pl*, gave no purples, while crosses of weak purple with purple, *A B Pl*, and with sun red, *A B pl*, gave purple, the *Pl pl* pair is not concerned in the difference between weak purple and purple any more than in that between weak purple and dilute purple. These results, however, do not exclude the possibility that weak purple may be *A b Pl*, like dilute purple, with the addition of some unknown dominant modifying factor.

A single weak purple plant, which was, so far as known, unrelated to the weak purples considered above, when crossed with two unrelated dilute sun reds gave progenies consisting of 15 weak purples and 13 weak sun reds. Seven progenies of these F_1 weak purple plants backcrossed

with dilute sun reds are listed in table 34, group 2. These progenies consisted of four color types, weak purple, weak sun red, dilute purple, and dilute sun red, in the numerical relations given below:

Color types	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	481	526	460	537	2,004
Calculated	501	501	501	501	2,004
Difference	—20	+25	—41	+36	0

The deviations from equality of the four classes expected of a dihybrid are so great that they would not occur by chance alone more than once in twenty trials, P equaling 0.05. Dr. Anderson's notes indicate that there was considerable difficulty, in the case of two of the cultures, in distinguishing dilute purple from dilute sun red. Whether this difficulty may account in part for the poor fit is not known. The outstanding fact, however, is the appearance of the four classes and no others. Since weak sun red is known to differ from dilute sun red by the factor pair B^w *b*, the inference is clear that weak purple differs from dilute purple by the same pair and by no others. The formulae assumed for the four color types are, therefore, *A* B^w *Pl*, *A* B^w *pl*, *A b Pl*, and *A b pl*, respectively.

If the foregoing conclusion is correct, crosses of weak sun reds with dilute purples should give weak purples in F_1 and the same four color classes in F_2 as are noted above for crosses of weak purple with dilute sun red. A single cross of a dilute purple with a homozygous weak sun red resulted in 18 weak purple plants. Two crosses of dilute purples with weak sun reds heterozygous for B^w *b* gave 12 weak purples and 11 dilute purples. That the production of weak purples in these crosses was not due to the *b* or *Pl* factors of the dilute purple parents is evidenced by the fact that crosses of the same dilute purple individuals with sun reds gave full purples in F_1. One of the F_1 weak purples, *A A* B^w *b Pl pl*, of the above crosses was backcrossed with dilute sun red, *A b pl*, with the result (table 34, group 3) shown below. The expected equality of the

four color types was closely approached in the results, χ^2 equaling 0.80. The comparison of observed with expected results follows:

Color types	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	21	28	22	27	98
Calculated	24.5	24.5	24.5	24.5	98
Difference	—3.5	+3.5	—2.5	+2.5	0

The progeny of a purple plant heterozygous for *B* B^w, *Pl pl*, and the endosperm color pair *Y y*, backcrossed with a white-seeded weak sun red plant, *A* B^w *pl y*, affords evidence of another kind with respect to the interrelations of strong and weak purple and of strong and weak sun red. It has been noted previously (page 60) that *Pl pl* and *Yy* are linked, with a somewhat irregular percentage of crossing-over. The backcross gave the four color types purple, weak purple, sun red, and weak sun red, in the numerical relation 60:48:59:62. The observed deviations from the equality expected of a dihybrid are such as might occur by chance more than once in two trials, P equaling 0.54. The distribution of these 229 plants to the four color types when the progeny of yellow seeds and that of white seeds are considered separately is as follows:

Color types	Purple Ia	Weak purple Ib	Sun red IIa	Weak sun red IIb	Total
Yellow seeds	48	36	8	17	109
White seeds	12	12	51	45	120

Evidently weak purple, assumed to be *A* B^w *Pl*, here bears the same relation to weak sun red, *A* B^w *pl*, that purple, *A B Pl*, is known to bear to sun red, *A B pl*. In case of the purples and the sun reds alone, the linkage of *Pl pl* with *Y y* is shown by 99 non-crossovers to 20 crossovers, or 16.8 ± 2.7 per cent of crossing-over. When the weak purples and the weak sun reds are alone considered, the non-crossovers are to the crossovers as 81:29, a crossover percentage of 26.4 ± 2.8. While the

difference between these two percentages of crossing-over, 9.6 ± 3.9, is considerable, it is probably not statistically significant, P equaling 0.09.

Still further evidence in favor of the assumption that weak purple is differentiated from dilute purple by the factor pair B^w *b*, just as weak sun red is differentiated from dilute sun red, is afforded by data from six of the progenies recorded in group 2 of table 34. These data, it will be recalled, were obtained from F_1's of weak purple x dilute sun red backcrossed to dilute sun red. The F_1 weak purples were heterozygous for liguleless leaf as well as for plant color, *A A* B^w *b Pl pl Lg lg*, and the dilute sun reds with which they were backcrossed were liguleless, *A b pl lg*. The 1724 plants were distributed as follows:

Color types	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa	Total
Normal leaves	296	315	119	164	894
Liguleless leaves	108	125	280	317	830

Evidently the linkage relations of liguleless with weak purple and dilute purple are similar to those already known for liguleless with weak sun red and dilute sun red (page 67). Of the 921 weak sun reds, *A* B^w *pl*, and dilute sun reds, *A b pl*, 632 belong to the non-crossover and 289 to the crossover class, a percentage of crossing-over of 31.4 ± 1.0. Similarly, of the 803 weak purples and dilute purples, the non-crossovers are to the crossovers as 576:227, a percentage of crossing-over of 28.3 ± 1.1. The difference between these two percentages of crossing-over, 3.1 ± 1.5, is such as might occur by chance once in six trials, P equaling 0.16.

By way of summary, it may be noted that, from appropriate intercrosses of the several color types and from determinations of the linkage relations of these types with liguleless leaf and with yellow endosperm, weak purple and weak sun red have been shown to have the genotypes *A* B^w *Pl* and *A* B^w *pl*, respectively. This establishes the existence of the triple allelomorphs, *B*, B^w, *b*. There is some evidence in favor of the occurrence of a fourth member of this series, b^s.

CROSSES INVOLVING THE MULTIPLE ALLELOMORPHS R^r, R^g, R^{rg}, r^r, r^g, r^{ch}

In an earlier section of this account (page 29) dealing with crosses involving only *A a*, *B b*, and *Pl pl*, three types of green plants were reported,

namely, *a B pl* (VIa), *a b Pl* (VIb), *a b pl* (VIc). Still another type of green — a type wholly devoid of purple, red, or brown pigment — has been used in several crosses, with results quite unlike those obtained from corresponding crosses with the other green types. For reasons that become apparent later, this fourth type of green is regarded as genetically similar to dilute sun red and is known as type IVg.

Green IVg x brown V

Generations F_1 and F_2.— When brown, *a B Pl*, is crossed with green of any of the three types previously studied, brown appears in F_1 and brown and green in F_2. If green VIc, *a b pl*, is used in the cross, the F_2 ratio approaches 9:7, while if green VIa, *a B pl*, or VIb, *a b Pl*, is used, 3:1 F_2 ratios are of course expected (tables 19 and 20, page 135). In striking contrast with such results are those obtained from a cross of brown with green IVg. Two such crosses gave 78 purple plants in F_1, and a third cross resulted in 72 purple and 63 sun red plants. It will be recalled that just such results as these were obtained from crosses of dilute sun red with brown (tables 4 and 14, pages 123 and 131). The brown plant, 2031–20, which gave purple and sun red F_1 plants when crossed with green IVg, was the identical plant previously reported (table 4, group 2) to have given 55 purples and 55 sun reds when crossed with a dilute sun red plant. Moreover, this same brown plant was shown (table 20, group 2, page 135) to have produced from self-pollination 82 browns and 34 greens. Evidently it was *a a B B Pl pl*. The important point here is that crosses of brown with green IVg give exactly the same results in F_1 as if green IVg were a dilute sun red, *A A b b pl pl*.

There are other reasons, in addition to the F_1 results of crosses with brown, for supposing that green IVg has the factor *A*. When the pericarp-color gene *P* occurs together with *A*, the resulting pericarp color is always red, but when *P* and *a a* are associated the pericarp color is brown. When green IVg plants have pericarp color it is red rather than brown, while that of greens VIa, VIb, and VIc is always brown. Again, the *A* factor is known to be essential to the production of aleurone color (Emerson, 1918), and the stock of IVg green plants used in these crosses, a strain of the variety Black Mexican sweet corn, was homozygous for purple aleurone. It is noteworthy in this connection that many, perhaps most, plants of this variety show very slight traces of sun red, and these traces are

limited commonly to the glumes of the staminate inflorescence. Apparently the stock of green IVg, which under no environmental conditions to which it has been subjected has ever been observed to produce the slightest trace of sun red, is merely an extreme minus variation of dilute sun red.

Not only were the F_1 results of the cross of brown with green IVg like those of the cross of brown with dilute sun red, but the same major color types appeared in F_2 (table 35, page 145). The distribution of all the individuals of six F_2 progenies to the six major color types heretofore recognized is compared below with the theoretical distribution calculated on the assumption that the green IVg parent was genotypically a dilute sun red, *A A b b pl pl*:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Observed.....	309	100	67	19	88	98	681
Calculated.....	287	96	96	32	96	74	681
Difference.....	+22	+4	—29	—13	—8	+24	0

The outstanding features of this comparison are the relatively small deviations, in comparison with the number of individuals, for the purple, sun red, and brown types, and the relatively large deviations for the dilute purple, dilute sun red, and green classes. The relative importance of the several deviations is best seen by a comparison of the quotients of calculated frequencies into the squares of corresponding deviations, from which χ^2 and P are derived (Elderton's and Pearson's tables). These quotients for the several classes are:

Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green
1.69	0.17	8.76	5.28	0.67	7.78

If these quotients were no greater in the case of dilute purple, dilute sun red, and green than for purple, sun red, and brown, there would be about two chances in five that the observed deviations might be due merely to errors of random sampling, a fairly good fit being shown — $\chi^2 = 5.06$, $P = 0.41$. But as they stand, these deviations could be expected to occur thru chance alone not more than once in five thousand similar trials, a

very poor fit being shown — $\chi^2 = 24.35$, $P = 0.0002$. Evidently, green IVg does not give the same results in F_2 of this cross as does dilute sun red.

It is to be supposed, of course, that green IVg differs in some essential genetic way from dilute sun red, else it would not remain true green for generation after generation while the typical dilute sun red constantly produces a conspicuous amount of sun red pigment. It was therefore to be expected that the dilute sun red class would be deficient in F_2 while the green class would show a corresponding excess. But if the 24 green plants in excess of the calculated number be added to the dilute sun red class, that class becomes too large by eleven individuals, the excess now becoming almost as great as the observed deficiency. Moreover, the dilute purple class, it must be remembered, remains greatly deficient. If it be supposed that the excess of greens came about at the expense of dilute purples as well as of dilute sun reds, a very good fit of observation to theory is obtained. On redistribution of the 24 greens in excess of expectation to the dilute purples and dilute sun reds in the 3:1 relation usually existing between these classes, the corrected distribution for the six classes is as shown below. There are almost two chances in five that the deviations may be due to random sampling, P equaling 0.38.

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Corrected distribution	309	100	85	25	88	74	681
Calculated	287	96	96	32	96	74	681
Difference	+22	+4	—11	—7	—8	0	0

Mere closeness of fit cannot, of course, be regarded as proof of the supposition on which the corrected distribution was made. But there are other considerations which greatly strengthen the hypothesis. In the case of all the F_2 progenies listed in table 35, it was observed that some of the purple plants, altho quite as strongly colored otherwise as normal purples, had wholly green anthers in place of the usual dark purple ones (Plate I, 4). Likewise some of the sun red plants had green instead of pink anthers. In striking contrast to this, not a single dilute purple or dilute sun red plant with green anthers was seen in the whole lot, the dilute

purples, so far as observed, having dark purple anthers and the dilute sun reds pink anthers, just as in the lots considered in the first section of this paper. Counts of the purple and the sun red plants with different anther colors were made for only three of the six F_2 progenies (table 36), and for these lots not every plant was noted at the time when it was possible to determine the anther color positively. When some anthers have become dry and weathered, it is impossible to tell whether they were pink or green when fresh. Less difficulty is experienced with purple anthers, which hold their color much longer. Unfortunately, the records of the three F_2 families were not made early enough for positive identification of anther color of all plants. Of 162 purple plants, 117 had purple anthers and 33 had green anthers, while 12 were not recorded. Of 50 sun red plants, 21 had pink anthers and 12 had green anthers, with 17 not recorded. In these two lots the plants with purple and pink anthers were together about three times as numerous as those with green anthers, thus suggesting a simple monohybrid relation between colored and green anthers.

Working hypothesis.— If the genetic factor which is responsible for green anthers of purple and sun red plants be assumed to cause, in the case of dilute purples and dilute sun reds, not merely the anthers but the whole plant — leaves, sheaths, husks, glumes, stalk, and so forth — to be green, a satisfactory working hypothesis is afforded. The factor concerned here has been found to be the well-known aleurone-color factor *R*, or else some factor very closely linked with it. Some of the evidence on which this statement is based is presented later in this paper (pages 80, 98). It may be pointed out in passing that the relation between anther color and aleurone color here noted was studied by Webber (1906) some years before the several aleurone-color and plant-color factors had been determined.

Since aleurone color is not primarily concerned in the present account, it might be less confusing if the case were regarded as one of complete linkage, and if some other symbol for anther color were used and all reference to the *R* factor omitted in this paper. Until recently there was nothing known of aleurone-color behavior that made necessary the assumption of more than the simple factor pair, *R r*. The plant-color behavior, on the other hand, as becomes apparent later, necessitates the assumption of a group of multiple allelomorphs responsible in turn for diverse combinations of colors of leaves, sheaths, anthers, silks, and other plant parts. The commonest combinations in the writer's cultures are

strong pink anthers with deep red silks, lighter pink anthers with reddish or pinkish silks, green anthers with green silks, and so on, but there exist also such combinations as strong pink anthers with green silks, green anthers with reddish silks, and the like. Moreover, different intensities of dilute sun red in leaf blades, glumes, and other parts are sometimes combined with various silk-color and anther-color combinations. There is evidence that at least several of these combinations behave as would be expected if each were a definite unit allelomorphic to any one of the others.

Perhaps the most remarkable feature of this series of allelomorphs — or supposed allelomorphs — is the fact that a single unit behaves as a dominant with respect to the color of one plant part and as a recessive with respect to that of another part. Thus, a combination of dominant pink anthers with recessive green silks is common in the writer's cultures. The wholly green plants used in the crosses here under consideration are recessive for green silks, anthers, glumes, sheaths, husks, and other parts, and dominant for colored aleurone. Since the aleurone-color symbols *R r* have long been employed in the usual way, *R* as the dominant and *r* as the recessive allelomorph, this usage is adhered to in this paper. The effect of these factors on plant color is indicated by superscripts. Thus, both R^r and r^r are dominant allelomorphs with respect to pink anthers and reddish silks, while both R^g and r^g are recessive for green anthers, silks, and so on. In the crosses here considered it is known that r^r and R^g are the pair concerned. With respect to plant color, therefore, as contrasted with aleurone color, r^r is dominant and R^g is recessive. While it is realized that this usage may tend to confuse the hasty reader, the use of any other symbols that have so far suggested themselves would result in greater confusion ultimately, particularly when the interrelations of plant color and aleurone color are taken up.

To return to the F_2 behavior of crosses of green IVg with brown, the following notation should express the F_2 results obtained, provided the proposed hypothesis is tenable:

Phenotypes	Plant color	Anther color
81 — *A B Pl* r^r — *Ia*	Purple	Purple
27 — *A B Pl* R^g — *Ig*	Purple	Green
27 — *A B pl* r^r — *IIa*	Sun red	Pink
9 — *A B pl* R^g — *IIg*	Sun red	Green
27 — *A b Pl* r^r — *IIIa*	Dilute purple	Purple

Phenotypes	Plant color	Anther color
9 — *A b Pl R*^{g} — *III g*	Green	Green
9 — *A b pl r*^{r} — *IV a*	Dilute sun red	Pink
3 — *A b pl R*^{g} — *IV g*	Green	Green
27 — *a B Pl r*^{r} — *V*	Brown	Green
9 — *a B Pl R*^{g} — *V*	Brown	Green
9 — *a B pl r*^{r} — *VI a*	Green	Green
3 — *a B pl R*^{g} — *VI a*	Green	Green
9 — *a b Pl r*^{r} — *VI b*	Green	Green
3 — *a b Pl R*^{g} — *VI b*	Green	Green
3 — *a b pl r*^{r} — *VI c*	Green	Green
1 — *a b pl R*^{g} — *VI c*	Green	Green
256		

The theoretical numerical relation between the several color combinations, in the order given above except that all greens are included in the last class, is 81:27:27:9:27:9:36:40, total 256.

The distribution of the 353 individuals of the three F_2 progenies for which anther records were made (table 36, page 146) is compared below with the theoretical distribution. In order that all plants may be included, the few purple and sun red plants whose anther colors were not noted are arbitrarily distributed to the colored-anther and green-anther classes in a 3:1 ratio. The fit of observation to hypothesis is so good that there are three chances in five that the deviations may be due to errors of random sampling, P equaling 0.60.

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Anther color	Purple	Green	Pink	Green	Purple	Pink	Green	Green	
	Ia	Ig	IIa	IIg	IIIa	IVa	V	IIIg, IVg, VI	
Observed.....	126	36	34	16	39	10	42	50	353
Calculated.....	112	37	37	12	37	12	50	55	352
Difference.....	+14	−1	−3	+4	+2	−2	−8	−5	+1

When the six F_2 progenies listed in table 35, for three of which no records of anther color were made, are grouped without reference to anther color, the comparison of observed and calculated numbers are as given below. For the six progenies there is practically an even chance that the deviations may be due to errors of random sampling, P equaling 0.48. It will be recalled that when these same progenies were compared with the dis-

tribution calculated on the basis of the three-factor hypothesis, the fit was very poor, P equaling 0.0002 (page 76). Comparison of the observed distribution with the distribution calculated on the four-factor basis follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green IIIg, IVg, VI	Total
Observed	309	100	67	19	88	98	681
Calculated	287	96	72	24	96	106	681
Difference	+22	+4	−5	−5	−8	−8	0

Relation of aleurone color to plant color.— It is evident from the comparisons already given that the four-factor hypothesis fits well the F_2 data, which is of course to be expected since it was invented for that purpose. But this fact alone is far from a substantiation of the hypothesis. The genetic tests ordinarily available are the behavior of the several F_2 types in later generations and in intercrosses. Since aleurone color as well as plant color is involved in these crosses, still another test can be employed. The six F_1 plants whose F_2 progenies are recorded in table 35 produced from self-pollination a total of 955 seeds, of which 388 had colored and 567 colorless aleurone. This obviously approaches closely a 27:37 ratio, the percentage of colorless seeds being 59.4 ± 1.1 while the theoretical percentage is 57.8 (Emerson, 1918). The deviation from expectation, 1.6 ± 1.1 per cent, is such as might be expected by chance once in three trials, P equaling 0.33. Evidently, therefore, the aleurone factors *A*, *C*, and *R* are concerned in these crosses. Since *A* and *R* are assumed by the hypothesis to be plant-color factors also, there is afforded opportunity of comparing the plant-color classes from colored with those from colorless seeds. Since colored aleurone requires the interaction of *A*, *C*, and *R*, colored seeds should never produce brown plants nor green plants of type VI, both of which are *a a*. As seen from the data given below, no brown plants came from colored seeds but a few wholly green plants appeared. Greens of type IVg are of course to be expected from seeds homozygous for R^g. Owing to the fact that a larger percentage of colorless than of colored seeds produced plants, the theoretical distribution with respect to plant color, given below, was calculated separately for colored and for colorless seeds. For the colored seeds there are nearly two chances in

five (P equaling 0.58), and for the colorless seeds only about one chance in fourteen (P equaling 0.07), that the observed deviations may be due to errors of random sampling. The comparisons follow:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green IIIg, IVg, VI	Total
Colored seeds:							
Observed	148	51	25	8	0	23	255
Calculated	143	48	32	11	0	21	255
Difference	+5	+3	—7	—3	0	+2	0
Colorless seeds:							
Observed	161	49	42	11	88	75	426
Calculated	136	45	39	13	104	89	426
Difference	+25	+4	+3	—2	—16	—14	0

It is noteworthy that the ratio of purples and sun reds to dilute purples and dilute sun reds is considerably greater for plants grown from colored seeds than for those from colorless seeds. This is to be expected from the fact that *R* must be present in all colored seeds, while some of the colorless seeds here concerned were doubtless *r r*. Hence, $R^g R^g$ should have occurred more frequently in the colored than in the colorless seeds, and should, by the hypothesis here under test, have reduced the numbers of dilute purples and dilute sun reds, causing these plants to appear as greens, types IIIg and IVg. If the 23 green plants grown from colored seeds are added to the dilute purples and dilute sun reds, the ratio of strong to dilute purples and sun reds approaches closely the ratio observed for the plants from colorless seeds.

It is even more instructive to note the relation of aleurone color to plant color in the case of the three F_2 lots for which anther colors were recorded (table 36, page 146). For this comparison the few purple and sun red plants whose anther colors were not recorded have been distributed to the colored-anther and green-anther classes in approximately the ratio in which these anther colors were found to occur in the cases in which anther colors were recorded. Since a larger proportion of colorless than of colored seeds produced plants, the theoretical distribution has been calculated separately for the two classes of seeds. The comparisons follow:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Anther color	Purple Ia	Green Ig	Pink IIa	Green IIg	Purple IIIa	Pink IVa	Green V	Green IIIg, IVg, VI	
Colored aleurone:									
Observed.....	48	25	11	12	16	4	0	10	126
Calculated.....	47	24	16	8	16	5	0	10	126
Difference.....	+1	+1	−5	+4	0	−1	0	0	0
Colorless aleurone:									
Observed.....	78	11	23	4	23	6	42	40	227
Calculated.....	62	10	21	4	21	7	55	47	227
Difference.....	+16	+1	+2	0	+2	−1	−13	−7	0

In view of the rather large number of plant-color classes and the comparatively small number of individuals concerned here, the fit of the observed to the theoretical distribution is remarkably good. The deviations are such as might be expected by chance seven times in ten trials for the colored-seeded lot (P = 0.70), and about once in four trials for the colorless-seeded lot (P = 0.26). In addition to this comparison of the lot as a whole, it should be noted that, while among the purple and sun red plants as a whole the expected relation of colored (purple and pink) anthers to colorless (green) anthers is 3:1, for the colored-seeded lot it is 2:1 and for the colorless-seeded lot it is 6:1. The observed relations were 59:37 and 101:15, or about 1.6:1 and 6.7:1, respectively. On the whole, therefore, this comparison, involving aleurone color as well as plant color, supports the suggested factorial interpretation.

Later behavior of F_2 purple I.— Only three F_2 purples with purple anthers were tested in F_3. One of these, 2960–9, resulted in purple plants with purple, Ia, and green, Ig, anthers, and sun red plants with pink, IIa, and green, IIg, anthers, in the respective numbers 14:9:6:3. A purple plant of the genotype $A\ A\ B\ B\ Pl\ pl\ R^g\ r^r$ should give these four classes in the relation 18:6:6:2. The observed deviations might be expected twice in five trials, P equaling 0.41.

Another F_2 purple plant, 2958–8, gave F_3 progeny consisting of the same eight color types as were seen in F_2 in table 36 (page 146). Evidently the F_2 purple plant was $A\ a\ B\ b\ Pl\ pl\ R^g\ r^r$. The deviations from expectation are such as might occur by chance in about seventeen out of any twenty such trials, P equaling 0.86. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Anther color	Purple	Green	Pink	Green	Purple	Pink	Green	Green	
	Ia	Ig	IIa	IIg	IIIa	IVa	V	IIIg, IVg, VI	
Observed	28	13	11	3	7	3	16	11	92
Calculated	29	10	10	3	10	3	13	14	92
Difference	−1	+3	+1	0	−3	0	+3	−3	0

The third purple-anthered F_2 purple tested, 2961–3, gave in F_3 all the color types except dilute purple, IIIa, and dilute sun red, IVa. A purple plant of the genotype $A\,a\,B\,B\,Pl\,pl\,R^g\,r^r$ should give the color types observed. The observed deviations from expectation might occur by chance about once in seven trials, P equaling 0.15. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Brown	Green	Total
Anther color	Purple	Green	Pink	Green	Green	Green	
	Ia	Ig	IIa	IIg	V	VI	
Observed	37	11	5	2	12	3	70
Calculated	30	10	10	3	10	8	71
Difference	+7	+1	−5	−1	+2	−5	−1

A single green-anthered F_2 purple, 2960–7, gave four F_3 color types, purple, sun red, brown, and green, all with green anthers. This behavior is to be expected from an F_2 genotype $A\,a\,B\,B\,Pl\,pl\,R^g\,R^g$. One of the F_3 purples, 4956–1, repeated this behavior in F_4. The F_3 and F_4 progenies are shown together in the following comparison, for which P = 0.60:

Color types	Purple	Sun red	Brown	Green	Total
	Ig	IIg	V	VI	
Observed	84	27	35	7	153
Calculated	86	29	29	9	153
Difference	−2	−2	+6	−2	0

It is of interest to note in this connection that a plant of the genotype $A\,a\,B\,B\,Pl\,pl\,R^g\,R^g$ could not exhibit a 27:37 ratio of colored to colorless aleurone, as was the case for some of the plants dealt with earlier.

For *A a* R^g R^g the aleurone-color ratio must be either 9:7 or 3:1, depending on whether the third aleurone-factor pair is *C c* or *C C*. The F_2 purple plant 2960–7 showed a 9:7 aleurone-color ratio with 86 colored and 74 colorless seeds, *A a C c R R*, while the F_3 plant 4956–1 exhibited a 3:1 ratio with 213 colored and 67 colorless seeds, *A a C C R R*. Another purple plant of the same F_3 progeny, 4956–32, exhibited a 3:1 aleurone-color ratio and threw only green-anthered purple and sun red plants. Its genotype must have been *A A B B C c Pl pl* R^g R^g. Thus it is often possible, from behavior in the following generation, to know the genotype not only with respect to plant color but for aleurone color as well. This is particularly true when the *B* factor is present.

Of the twenty-four sorts of behavior possible, according to hypothesis, for F_2 purples of the cross under consideration, four sorts have been exhibited in F_3 and a fifth shown in F_4. This is far from an adequate study of the F_2 purples. All that can be claimed, therefore, is that, so far as they go, the results are in accord with the hypothesis.

Behavior of other F_2 color types.— Only one F_2 sun red plant with pink anthers, 2961–4, was tested in F_3. It produced sun reds with pink and sun reds with green anthers, dilute sun reds, and greens. Since anther color was noted for only a part of the plants, it has to be disregarded in classifying the F_3 progeny. The color types sun red, dilute sun red, and green occurred in the numerical relation 114:23:57. Of the eight possible genotypes of pink-anthered sun red, only three could throw these three color classes — *A a B b* r^r r^r, *A A B b* R^g r^r, and *A a B b* R^g r^r. From the first genotype a 9:3:4, from the second a 12:3:1, and from the third a 36:9:19, relation should exist between the F_3 classes. The poor fit of observed numbers to the 9:3:4 relation makes it improbable that the first genotype is concerned, there being only about one chance in twenty-two that the observed deviations are due to errors of random sampling, P equaling 0.045. The comparison follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed	114	23	57	194
Calculated	109	36	49	194
Difference	+5	—13	+8	0

A more conclusive reason for throwing out the first genotype is the fact that the plant had some seeds with colored aleurone, which would have been impossible if it were $r\,r$. The second genotype is discarded because of the extremely poor fit of observed numbers to the 12:3:1 relation. There is an almost inconceivably small chance that the observed deviations may be due to errors of random sampling, χ^2 equaling 180. (When $n' = 3$ and $\chi^2 = 29$, $P = 0.000001$. Higher values of χ^2 when $n' = 3$ are not listed in Pearson's tables.) The comparison follows:

Color types	Sun red IIa, g	Dilute sun red IVa	Green IVg	Total
Observed	114	23	57	194
Calculated	146	36	12	194
Difference	—32	—13	+45	0

The elimination of the first two genotypes leaves the third genotype as the only one that can be concerned here. The fit of observed numbers to the 36:9:19 relation is very close, χ^2 equaling 0.84. (Values of P are not listed in Pearson's tables for values of χ^2 less than 1; when $\chi^2 = 1$ and $n' = 3$, $P = 0.61$.) The comparison follows:

Color types	Sun red IIa, g	Dilute sun red IVa	Green IVg, VIa, c	Total
Observed	114	23	57	194
Calculated	109	27	58	194
Difference	+5	—4	—1	0

This comparison leaves little doubt that the genotype of the F_2 plant concerned is $A\,a\,B\,b\,R^g\,r^r$. There are, moreover, other considerations which go far toward identifying the genotype as given here. The fact that some sun red plants of F_3 had green and others pink anthers is evidence for the constitution $R^g\,r^r$. Since dilute sun red plants appeared in F_3, there can be no question as to $B\,b$. The F_2 plant showed a 9:7 aleurone-color segregation, and therefore, in addition to $R\,r$, it must have been

either *A a* or *C c*. An F_3 sun red plant with green anthers, $R^g R^g$, had 97 colored and 20 colorless seeds, again indicating either *A a* or *C c*. If it was *A A B b C c* $R^g R^g$, both colored and colorless seeds should have given sun red and green plants in a 3:1 ratio; if it was *A a B B C C* $R^g R^g$, the colored seeds should have given sun red and the colorless ones green plants only, the plant-color ratio again being 3:1; but if it was *A a B b C C* $R^g R^g$, the colored seeds should have produced sun red and green plants in a 3:1 ratio and the colorless seeds green plants only, the ratio of sun reds to greens in the two lots together being 9:7. Actually the colored seeds resulted in 23 sun red and 10 green plants and the colorless seeds in 10 green plants only, the ratio of sun reds to greens being 23:20, thus approaching 9:7. There is, therefore, considerable assurance that the F_3 plant was *A a B b C C* $R^g R^g$, that the F_2 plant was *A a B b C C* $R^g r^r$, and that the F_3 numerical relation of plant colors was 36:9:19, as originally suggested by the closeness-of-fit test.

A single dilute purple plant of F_2, 2960–4, was tested in F_3 and found to give 38 dilute purple and 39 green plants. Of the eight possible genotypes for F_2 dilute purples, the only ones that could give only dilute purples and greens in F_3 are *A A b b Pl Pl* $R^g r^r$, *A a b b Pl Pl* $r^r r^r$, and *A a b b Pl Pl* $R^g r^r$. The first two should give a 3:1, and the third a 9:7, F_3 ratio. The plant had colored aleurone, which throws out of consideration the second genotype with *r r*. The F_3 plant-color ratio fits fairly well a 9:7 but not at all a 3:1 expectation, the observed numbers being 38:39 and the calculated numbers 43:34 and 58:19, with deviations of 5 and 20, and probable errors of 2.6 and 2.9, respectively. The deviation from a 9:7 ratio might occur by chance once in five trials, P equaling 0.20, but that from a 3:1 ratio not more than twice in about a million trials, P equaling 0.000002. The genotype *A a b b Pl Pl* $R^g r^r$ is therefore decidedly favored by these results. The aleurone-color record shows that this genotype is possible, since there were 57 colored and 56 colorless seeds, a relation about halfway between the 9:7 and the 27:37 ratio due to *A a C C R r* and *A a C c R r*, respectively.

Intercrosses of F_2 color types

It is realized that the tests of F_2 types by studies of their behavior in later generations as reported above, are markedly inadequate to serve

as a demonstration of the hypothesis suggested to account for the F_2 behavior of the cross of brown, type V, with green, type IVg. It is noteworthy, however, that no results have been found that do not agree with the hypothesis. Fortunately, several intercrosses of the types found in F_2 afford additional evidence.

Purple Ig x green VIc.— Green-anthered purples, *A B Pl* R^g, crossed with greens of type VIc, *a b pl* r^r, should give F_2 results identical with those found from the original cross of brown, *a B Pl* r^r, with green of type IVg, *A b pl* R^g, since F_1 in either case should be *A a B b Pl pl* R^g r^r. Two such crosses are recorded in table 37, group 1 (page 146). The F_1 plants were both purple, with purple anthers. In F_2 the same eight types were noted as in F_2 of the cross of brown with green IVg (table 36). The anther color was not recorded, however, for many of the plants, so that only six color classes are shown, as in table 35. While all the expected color types are present, the fit of observed to calculated numbers is so poor that the observed deviations should not occur by chance more than once in thirty trials, P equaling 0.033. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia, g	IIa, g	IIIa	IVa	V	IIIg, IVg, VI	
Observed....	80	13	9	9	20	27	158
Calculated...	66	22	17	6	22	25	158
Difference...	+14	—9	—8	+3	—2	+2	0

If, notwithstanding the poor fit shown above, the F_1 was *A a B b Pl pl* R^g r^r, a backcross of F_1 with green of type VIc, *a b pl* r^r, should result in the same six major plant-color types, but no green-anthered purples or sun reds should occur. Such crosses are listed in group 2 of table 37. All the purple plants had purple anthers and all the sun red plants had pink anthers. Moreover, the six color classes appeared in so very nearly the expected relation of 1:1:1:1:1:3 that deviations as great as those observed might be expected to occur by chance perhaps ninety-nine times in one hundred trials, χ^2 equaling 0.85 (when $\chi^2 = 1$ and $n' = 6$, $P = 0.96$). The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VI	
Observed.....	36	29	31	31	31	95	253
Calculated.....	31.6	31.6	31.6	31.6	31.6	94.9	252.9
Difference.....	+4.4	—2.6	—0.6	—0.6	—0.6	+0.1	+0.1

If an F_1 supposedly *A a B b Pl pl* $R^g r^r$, be backcrossed to dilute sun red, type IVa, *A b pl* r^r, color types Ia, IIa, IIIa, and IVa should appear, none of them with green anthers. Such crosses are presented in group 3 of table 37. The anthers thruout were purple or pink, and the several color types appeared in approximately equal numbers, as expected, there being more than two chances in five that the observed deviations may have been due to errors of random sampling, P equaling 0.42. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed.....	115	97	95	111	418
Calculated.....	104.5	104.5	104.5	104.5	418
Difference.....	+10.5	—7.5	—9.5	+6.5	0

If the same F_1 genotype, *A a B b Pl pl* $R^g r^r$, be backcrossed with green of type IVg, *A b pl* R^g, there should occur five major color types, brown not appearing, and both green and colored anthers should be found in both the purple and the sun red plants. The records of such a cross are given in group 4 of table 37. The seven expected color types occurred in numbers near enough to expectation so that there are nearly three chances in ten that the deviations may have been due to errors of random sampling, P equaling 0.29. The most pronounced deviations are the excess of dilute sun reds and the deficiency of greens. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Green	Total
Anther color	Purple	Green	Pink	Green	Purple	Pink	Green	
	Ia	Ig	IIa	IIg	IIIa	IVa	IIIg, IVg	
Observed.....	10	13	7	8	10	15	13	76
Calculated.....	9.5	9.5	9.5	9.5	9.5	9.5	19	76
Difference.....	+0.5	+3.5	—2.5	—1.5	+0.5	+5.5	—6	0

In conclusion it seems safe to say that the cross of green-anthered purple, Ig, with green of type VIc, has given results similar to those yielded by the cross of brown, V, with green of type IVg. Since this was to have been expected from the hypothesis suggested by the F_2 generation of the latter cross, the results just discussed lend support to that hypothesis.

Purple Ig x dilute sun red IVa.— In accordance with the hypothesis under consideration, green-anthered purple is *A B Pl* R^g and dilute sun red is *A b pl* r^r. F_1 of the cross should be *A A B b Pl pl* R^g r^r, and F_2 should consist of the five major color types, purple, sun red, dilute purple, dilute sun red, and green of types IIIg and IVg, with both green-anthered and colored-anthered subclasses of purples and sun reds. The F_1 plants were purple-anthered purples, as expected. Three F_2 progenies are recorded in table 38, group 1. Anther color could not be recorded in all cases, but in each of the three F_2 progenies both green and colored anthers were noted for both purple and sun red plants. In one progeny, 5042–5045, of a total of 57 purples and sun reds, 41 had colored and 16 had green anthers, which is not far from the expected 3:1 relation. The 415 F_2 plants were so distributed among the five color classes that the chances are nearly three in five that the deviations observed may have been due to errors of random sampling, P equaling 0.58. A comparison of observed and theoretical distributions follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Green	Total
	Ia, g	IIa, g	IIIa	IVa	IIIg, IVg	
Observed	243	71	59	22	20	415
Calculated	234	78	58	19	26	415
Difference	+9	—7	+1	+3	—6	0

An F_1 of the cross here considered, 6557–12, *A A B b Pl pl* R^g r^r, was backcrossed to a dilute sun red, *A b pl* r^r. Four color types occurred in the progeny, as expected, and all the plants had colored anthers. The deviations from expectation were such as might occur by chance in considerably more than one out of any two such trials, P equaling 0.56. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	43	43	35	48	169
Calculated	42	42	42	42	168
Difference	+1	+1	—7	+6	+1

Purple Ia x green IVg.— The cross between purple Ia and green IVg should have given results identical with those expected from the cross of green-anthered purple with dilute sun red. The parents are supposed to have been *A B Pl* r^r and *A b pl* R^g, and the F_1, therefore, *A A B b Pl pl* R^g r^r. The F_1's were purple-anthered purples. Two F_2 progenies are listed in table 38, group 2. All the expected color types occurred, but the observed frequency distribution was such as might be expected to occur by chance only about once in eleven trials, P equaling 0.09. If these progenies are grouped into five classes, anther color being disregarded, the fit is somewhat better, P equaling 0.16. The comparison of observed and theoretical frequencies follows:

Plant color / Anther color	Purple Purple Ia	Purple Green Ig	Sun red Pink IIa	Sun red Green IIg	Dilute purple Purple IIIa	Dilute sun red Pink IVa	Green Green IIIg, IVg	Total
Observed	26	14	17	3	9	2	1	72
Calculated	31	10	10	3	10	3	5	72
Difference	—5	+4	+7	0	—1	—1	—4	0

The F_2 of this cross exhibited, as expected, practically the same results as were obtained from the cross of green-anthered purple with dilute sun red. Unlike that cross, the one under consideration here was checked by the behavior of some of its F_2 types in later generations.

A single F_2 purple-anthered purple produced in F_3 16 plants (table 39, group 1), including only purple, sun red, and dilute purple in the relation 9:4:3. Of both the purples and the sun reds, some plants had colored and some had green anthers. Obviously two other types, dilute sun red and green, should occur in such an F_3 and doubtless would have been found had a larger number of plants been grown, for the F_2 plant, in order to have produced the color types recorded, must have been *A A B b Pl pl* R^g r^r.

Only one plant of each of the missing classes was to have been expected, and the distribution as a whole was not far from expectation, P equaling 0.59. Both the types lacking in F_3 occurred in F_4, a pink-anthered sun red F_3 producing sun reds and dilute sun reds, while green-anthered purples produced in one instance purples, sun reds, and greens, and in another instance purples and greens only, all with green anthers. This F_3 lot may consequently be regarded as $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$, and therefore equivalent to the F_2 lot from which it came, and its F_4 progenies equivalent to F_3 progenies.

A second F_2 purple-anthered purple was backcrossed to green plants of types IVg and VIc (group 1, table 39). From the backcross with green of type IVg, $A\ b\ pl\ R^g$, five major color types appeared and both the purple and the sun red types contained subtypes with colored and with green anthers. While all the classes expected from an F_2 of the genotype $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$ occurred, the frequency distribution was so far from expectation that there is only one chance in five hundred that the observed deviations may have been due to errors of random sampling, P equaling 0.002. The expected and observed distributions are as follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Green	Total
	Ia, g	IIa, g	IIIa	IVa	IIIg, IVg	
Observed	15	15	5	1	9	45
Calculated	9	9	9	9	9	45
Difference	+6	+6	—4	—8	0	0

Whether the discrepancy is genetically significant or was due to some accident of pollination cannot now be determined. A backcross of the same F_2 plant with green of type VIc, $a\ b\ pl\ r^r$, yielded only four color types, as expected (group 1, table 39), the anthers being colored in all cases. The excess of purples and deficiency in two other classes makes the deviations from expectation fairly great, so that there is only about one chance in seven that they may have been due to errors of random sampling, P equaling 0.14. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	27	19	15	14	75
Calculated	19	19	19	19	76
Difference	+8	0	—4	—5	—1

A third purple-anthered purple, an F_3 plant of the lot regarded as equivalent to F_2's, gave in the next generation purple-anthered purples and pink-anthered sun reds in the relation 31:7 (group 2, table 39). From the genotype *A A B B Pl pl r^r r^r*, these two phenotypes should appear in a 3:1 ratio. The deviation from expectation was 2.5 ± 1.8, or only such as might be expected about once in three trials, P equaling 0.34.

Two green-anthered purples of F_2 and two of the equivalent F_3 lot noted above were tested by a later generation. Two of the four yielded three color types, purple, sun red, and green, all with green anthers (group 3, table 39). Such behavior is expected from the genotype *A A B b Pl pl R^g R^g*. The 9:3:4 relation is approached so closely that the value of P cannot be determined from Pearson's tables, x^2 equaling 0.36. The comparison follows:

Color types	Purple Ig	Sun red IIg	Green IIIg, IVg	Total
Observed	37	11	14	62
Calculated	36	12	16	64
Difference	+1	—1	—2	—2

The same two green-anthered purples were backcrossed with green of type IVg, and one of them and a sib of the other with green of type VIc, with results as shown in group 3 of table 39. The crosses with type IVg, *A b pl R^g*, gave the same three classes as did the self-pollinations, and the frequency distribution differed from expectation by values that might occur by chance about once in two trials, P equaling 0.49. The comparison follows:

Color types	Purple Ig	Sun red IIg	Green IIIg, IVg	Total
Observed	34	32	53	119
Calculated	30	30	60	120
Difference	+4	+2	—7	—1

The backcrosses of these green-anthered purples with green of type VIc, *a b pl* r^r, as was to be expected, gave very different results. There were produced four instead of three phenotypes, all with colored (purple or pink) instead of green anthers. The deviations from the theoretical frequency distribution are such as might be expected about once in five trials, P equaling 0.21. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	44	48	33	52	177
Calculated	44	44	44	44	176
Difference	0	+4	—11	+8	+1

The other two green-anthered purples that were tested yielded only two phenotypes, green-anthered purple and green, in the relation 56:18 (group 4, table 39). The genotype *A A B b Pl Pl* R^g R^g should give these two phenotypes in a 3:1 ratio. The deviation from expectation was therefore 0.5 ± 2.5. One of the same plants backcrossed to green of type IVg gave 28 green-anthered purples and 27 greens where equality was expected.

Of the twelve kinds of behavior expected of F_2 purples of the cross of purple-anthered purple with green IVg, only four have been demonstrated. So far as they go, however, the results are quite in accord with the hypothesis under test. In addition to the F_2 purples, sun reds and dilute purples also were tested by later generations, as detailed below.

Three pink-anthered sun reds gave sun reds and dilute sun reds only, all with pink anthers (table 40, group 1). These three plants are therefore regarded as *A A B b pl pl* r^r r^r. The ratio observed was 97:26. The deviation from the expected 3:1 ratio was 4.75 ± 3.24, or such as might

occur by chance once in three trials, P equaling 0.32. One of these three sun reds, when crossed with a dilute purple, *A b Pl* r^r, gave 71 purples and 77 dilute purples, all with purple anthers, where equal numbers were expected.

Three other F_2 pink-anthered sun reds produced nothing but sun red plants in F_3, 228 in all (group 2, table 40). Some plants of each progeny had pink and some had green anthers. Small plantings of each lot were made in the garden and larger plantings in the field. Anther color was noted in the case of the garden plants only. The records show 44 with pink and 16 with green anthers, a deviation from a 3:1 ratio of only 1.0 ± 2.3. The F_2 sun reds are therefore assumed to have been *A A B B pl pl* R^g r^r. One of these F_2 plants was backcrossed to green, both of type IVg and of type VIc, resulting in a total of 108 sun red plants (group 2). Altho no counts were made for anther color, it was noted that the cross with green IVg, *A b pl* R^g, gave both pink- and green-anthered plants, while the cross with green VIc, *a b pl* r^r, gave pink anthers alone. Only two of the six possible genotypes of F_2 sun reds were demonstrated.

Only one dilute purple F_2 plant was tested further (group 3, table 40). From self-pollination it yielded 46 dilute purple and 9 dilute sun red plants, all with colored (purple or pink) anthers. The deviation from a 3:1 ratio, 4.75 ± 2.17, is such as might be expected by chance about once in seven trials, P equaling 0.14. The same F_2 plant when backcrossed to green of types IVg and VIc (group 3) gave 85 dilute purples and 82 dilute sun reds where equality was expected. Evidently this F_2 was *A A b b Pl pl* r^r r^r.

No F_2 dilute sun red or green plants were tested further. One F_3 dilute sun red, however, was found to breed true, producing an F_4 of 30 pink-anthered dilute sun reds. Likewise, eight F_3 and F_4 greens gave a total of 126 green plants in the next generation.

In so far as tests have been made, therefore, the cross of purple-anthered purple with green IVg has behaved as expected on the basis of the hypothetical genotype assigned to F_1, namely, *A A B b Pl pl* R^g r^r.

Purple Ig x green IVg.— Green-anthered purples are assumed to be *A B Pl* R^g, and green IVg to be *A b pl* R^g. The F_1 genotype is therefore, theoretically, *A A B b Pl pl* R^g R^g, and F_2 should consist of the three color types purple, sun red, and green, all with green anthers. Eight such F_2 progenies are recorded in table 41, group 1. The three types

occurred in so nearly the expected relation of 9:3:4 that the observed deviations might be expected by chance considerably more than once in three trials, P equaling 0.37. The comparison follows:

Color types	Purple Ig	Sun red IIg	Green IIIg, IVg	Total
Observed	293	105	150	548
Calculated	308	103	137	548
Difference	—15	+2	+13	0

The F_2 greens of this cross are assumed to consist of the genotypes *A b Pl* R^g and *A b pl* R^g, which, if r^r had been present instead of R^g, would have been dilute purples and dilute sun reds, respectively. In substantiation of this assumption, crosses of F_1's, all green-anthered purples, with dilute sun red, *A b pl* r^r, and with green VIc, *a b pl* r^r, are recorded in group 2 of table 41. As expected, the result was the four classes purple, sun red, dilute purple, and dilute sun red, all with colored anthers. The expected numerical equality of the four classes was so closely approached that deviations such as those observed might be expected by chance in nearly three out of four trials, P equaling 0.74. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	58	61	62	70	251
Calculated	63	63	63	63	252
Difference	—5	—2	—1	+7	—1

Still another F_1 was crossed with a pink-anthered sun red, *A B pl* r^r, and gave 68 purples and 67 sun reds, all with colored anthers, where equal numbers were expected.

So far as tested, therefore, the cross of green-anthered purple with green IVg has given the results expected on the basis of the hypothesis under test.

Purple Ig x brown V.— A cross of green-anthered purple, *A B Pl* R^g, with brown, *a B Pl* r^r, gave in F_1 49 purple-anthered purples, presumably

A a B B Pl Pl R^g r^r. An F_2 progeny was grown from only one F_1 plant, 6653–6, resulting in two major color types, purple and brown, in approximately a 3:1 ratio. The purples were, as expected, of two subtypes, one with purple and the other with green anthers. The theoretical relation of 9:3:4 was realized so closely that the observed deviations might be expected by chance in at least two out of three trials, χ^2 equaling 0.76 (when $\chi^2 = 1$ and $n' = 3$, $P = 0.61$). The comparison follows:

Color types	Purple, purple anthers Ia	Purple, green anthers Ig	Brown V	Total
Observed	23	5	9	37
Calculated	21	7	9	37
Difference	+2	—2	0	0

A second F_1 plant, 6653–2, was backcrossed with green IVg, *A b pl R^g*, resulting in 39 purple plants, 21 with purple and 18 with green anthers, where equal numbers were expected, the deviation from expectation being 1.5 ± 2.1. The same F_1 plant was crossed with a heterozygous dilute sun red, *A a b b pl pl r^r r^r*, resulting in 45 purple-anthered purples and 18 browns, the deviation from the expected 3:1 ratio being 2.25 ± 2.32.

Purple Ig x dilute purple IIIa.— Crosses of green-anthered purple, *A B Pl R^g*, with dilute purple, *A b Pl r^r*, gave in F_1 purple-anthered purple, *A A B b Pl Pl R^g r^r*. The F_2 should consist of purple-anthered and green-anthered purples, dilute purples, and greens, the three major color types appearing in the relation 12:3:1. In F_2 from a single F_1 plant, 5263–3, both purple-anthered and green-anthered purples were noted, but detailed counts based on anther color were not made. The deviations from the expected numbers for the three major types were such as might occur by chance in nine out of twenty such trials, P equaling 0.45. The comparison follows:

Color types	Purple Ia, g	Dilute purple IIIa	Green IIIg	Total
Observed	36	11	5	52
Calculated	39	10	3	52
Difference	—3	+1	+2	0

A second F_1 plant backcrossed with green IVg, *A b pl* R^g, gave the expected four types. The deviations from the equal frequency expected for the several types was such as might occur by chance somewhat more than once in four trials, P equaling 0.27. The comparison follows:

Color types	Purple, purple anthers Ia	Purple, green anthers Ig	Dilute purple IIIa	Green IIIg	Total
Observed...	59	67	80	77	283
Calculated..	71	71	71	71	284
Difference..	—12	—4	+9	+6	—1

Dilute purple IIIa x green IVg.— A single cross of dilute purple, *A b Pl* r^r, with green IVg, *A b pl* R^r, gave dilute purple, *A A b b Pl pl* R^g r^r, in F_1, and three phenotypes, dilute purple, dilute sun red, and green, in F_2 (table 42, group 1, page 150). The observed frequencies were 23:8:10, which is the nearest possible approach to the expected 9:3:4 relation for a total of 41 individuals. One F_2 dilute purple gave similar results in F_3, indicating the same genotype as the F_1 dilute purples. The F_4 progenies of this F_3 lot may be regarded as equivalent to F_3's, and are therefore grouped with the F_3 in table 43. Three F_3 and F_4 progenies (table 43, group 1A) approached the 9:3:4 relation so closely that the observed deviations might occur by chance in nearly three out of five trials, P equaling 0.59. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Observed.....	143	48	73	264
Calculated.....	149	50	66	265
Difference.....	—6	—2	+7	—1

The green plants of these F_3 and F_4 lots, as well as those of the F_2 lot listed in group 1 of table 42, are assumed to be *A b Pl* R^g and *A b pl* R^g, and consequently to differ from the dilute purples and dilute sun reds only in having R^g R^g in place of R^g r^r or r^r r^r. That the *R r* pair is thus concerned in these results can be shown by a comparison between the plant-

color phenotypes resulting from seeds with colored aleurone and those from seeds with colorless aleurone. The F_2 progeny came from a plant that produced from self-pollination colored and colorless seeds in the relation 60:24. This close approach to a 3:1 ratio indicates that the F_1 plant could have been heterozygous for only one of the aleurone-factor pairs *A a*, *C c*, or *R r* (Emerson, 1918). A cross with a *C* tester, *A c R*, resulted in 43 colored and no colorless seeds, while a cross with an R tester, *A C r*, gave 46 colored and 32 colorless seeds, thus indicating *R r* as the factor pair concerned. The colorless seeds must therefore have been *r r*, presumably $r^r\ r^r$, and in accordance with the hypothesis under test should have produced no green plants. Some of the colored seeds, on the contrary, should have been *R R*, supposedly $R^g\ R^g$, and these should have given green plants. For the most part, the colored and the colorless seeds were planted separately. The 9:3:4 relation of the three plant-color types is theoretically made up of a 6:2:4 relation from colored seeds and a 3:1:0 relation from colorless seeds. Actually, from colorless seeds there appeared dilute purple and dilute sun red plants in the ratio 69:15. The deviation from expectation, 6.0 ± 2.7, might be expected to occur about once in seven trials, P equaling 0.14. From colored seeds the deviation from the theoretical distribution was such as might occur thru errors of random sampling almost once in four trials, P equaling 0.23. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Observed	92	42	70	204
Calculated	102	34	68	204
Difference	−10	+8	+2	0

Aleurone is in some cases self-colored and in some cases mottled. Mottled aleurone ordinarily occurs only when the *R* factor is heterozygous, but not all heterozygous individuals are mottled (Emerson, 1918). Mottled seeds of the cross under discussion, just as colorless ones, since they are presumably $R^g\ r^r$, should produce no green plants. In the case of some of the progenies noted above, the colored seeds were sorted into self-colored, mottled, and colorless. Since usually about one-third

of the colored seeds are mottled, the 9:3:4 relation of plant-color types observed in this cross should be made up of a 3:1:0 relation from colorless seeds, 3:1:0 from mottled seeds, and 3:1:4 from self-colored seeds. Of the progenies for which the seeds were sorted in this way, the colorless seeds produced dilute purple and dilute sun red plants in the relation 60:14, with a deviation from 3:1 of 4.5 ± 2.5, the mottled seeds gave the same plant-color types in the relation 30:12, with a deviation of 1.5 ± 1.9, and the self-colored seeds yielded dilute purple, dilute sun red, and green in the relation 48:19:64 (the theoretical distribution for a total of 131 individuals is 49:16:66), the deviations being such as might occur by chance perhaps three times in four trials, x^2 equaling 0.64. On the whole, therefore, these crosses, and particularly the interrelations of aleurone and plant colors, afford strong evidence in support of the hypothesis under test.

Before presenting further F_3 results from these crosses, it may be well to consider other crosses of dilute purple with green IVg which, so far as plant color alone is concerned, have given results quite like those presented above but which exhibit a wholly different relation between plant color and aleurone color. The green plants concerned in these other crosses were *C* testers for aleurone color (Emerson, 1918), and were therefore known to be *A c R*, presumably *A c* R^g. The dilute purple plants concerned were homozygous for aleurone color, and were consequently *A C R*, presumably *A c* R^r. These crosses differ, then, from the ones discussed above in having R^r in place of r^r and *c* in place of *C*. Since the *C c* pair is supposed not to have any relation to plant color, the results for plant color should be quite like those for the other cross and there should be no relation between plant color and aleurone color. The results for F_2 are presented in table 42, group 2, and the F_3 results in table 43, group 1B. The three plant-color types appeared in F_2 in the relation 328:113:148, and in F_3 in the relation 40:14:23. Considered together these lots deviated very slightly from expectation, x^2 equaling 0.31. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Observed	368	127	171	666
Calculated	375	125	166	666
Difference	—7	+2	+5	0

The seeds from which these plants were grown consisted of colored and colorless in approximately a 3:1 ratio, as is expected when the *C* factor alone is heterozygous. The deviations from the expected 9:3:4 relation for plants from colored seeds was such as might occur by chance more than once in three trials, P equaling 0.36, and for plants from colorless seeds such as might occur once in six trials, P equaling 0.17. The comparisons follow:

Plant-color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Colored seeds:				
Observed	215	58	89	362
Calculated	204	68	90	362
Difference	+11	—10	—1	0
Colorless seeds:				
Observed	65	32	32	129
Calculated	73	24	32	129
Difference	—8	+8	0	0

The results presented for plant color alone and in relation to aleurone color in these crosses are therefore quite in keeping with the hypothetical constitution assigned to the F_1 plants, namely, *A A b b Pl pl* $R^r R^g$ *C c*, just as the results from the other crosses were in keeping with the assumed genotype *A A b b Pl pl* $R^g r^r$ *C C* for their F_1 plants.

A single F_1 plant was backcrossed with green IVg, *A b pl* R^g, with results as shown in table 42, group 3. The three color types dilute purple, dilute sun red, and green, occurred in the relation 46:45:86. The expected distribution for a total of 177 individuals is 44:44:89, showing almost a perfect fit, χ^2 equaling 0.21.

For both the lots of crosses under discussion, further tests are afforded by the behavior in F_3 and F_4. As already shown, some of the F_2 dilute purples had the same genetic constitution as the F_1 plants (table 43, groups 1A and 1B). The progenies of two other dilute purples, one of F_2 and the other of an equivalent F_3, produced dilute purple and dilute sun red plants only (group 2, table 43), in the relation 82:23. The devia-

tion from a 3:1 ratio is 3.25 ± 2.99. From their behavior and in view of the crosses in which they occurred, one of these plants is assumed to have been *A A b b Pl pl r^r r^r* and the other *A A b b Pl pl R^r R^r*.

A single dilute purple of an F_3 lot equivalent to an F_2 gave dilute purple and green plants only (group 3, table 43). The two color types appeared in the ratio 62:16, a deviation from 3:1 of 3.5 ± 2.6. The F_3 plant is therefore assumed to have been *A A b b Pl Pl R^g r^r*. Colorless and mottled seeds produced dilute purple plants only, as was expected. From self-colored seeds there resulted dilute purple and green plants in the relation 26:16, a deviation of 2.0 ± 2.0 from the expected 2:1 ratio.

Two dilute sun red plants gave progenies of dilute sun reds and greens in the relation 63:22, a deviation from a 3:1 ratio of 0.75 ± 2.69 (group 4, table 43). Presumably these plants were *A A b b pl pl R^g r^r* and *A A b b pl pl R^r R^g*. Four other dilute sun red plants bred true in the next generation (group 5, table 43), producing a total of 197 dilute sun red plants. These plants are therefore assigned the genotype *A A b b pl pl r^r r^r*.

Seven green plants likewise bred true (group 6, table 43), producing a total of 130 green plants. These plants were presumably *A b pl R^g* and *A b Pl R^g*.

To summarize, all types of behavior were observed in F_3 and equivalent F_4 generations of the cross of dilute purple with green IVg except true-breeding dilute purples. Only eight dilute purples were tested, and only one in nine is expected to breed true.

Sun red IIg and IIa and dilute sun red IVa x green IIIg and IVg.— Two crosses of green-anthered sun red with green IVg gave green-anthered sun red plants in F_1, theoretically *A A B b pl pl R^g R^g*. The parent types only appeared in F_2 (table 44, group 1). The observed numbers of green-anthered sun reds and greens were, respectively, 216 and 77. The deviation from the expected 3:1 ratio was 3.7 5± 5.00.

A cross of pink-anthered sun red with green IVg gave pink-anthered sun red in F_1, theoretically *A A B b pl pl R^g r^r*. F_1 plants backcrossed with green IVg, *A b pl R^g*, gave three major plant-color types (group 2, table 44) — sun red, dilute sun red, and green — with the sun reds appearing in two subtypes, one pink-anthered and the other green-anthered. Theoretically the four types should have been represented by an equal number of individuals. The deviations from this expectation were such

that there is considerably more than an even chance that they might have been due to errors of random sampling, P equaling 0.56. The comparison follows:

Color types	Sun red, pink anthers IIa	Sun red, green anthers IIg	Dilute sun red IVa	Green IVg	Total
Observed.....	105	90	105	109	409
Calculated.....	102	102	102	102	408
Difference.....	+3	—12	+3	+7	+1

Crosses of dilute sun red with green IVg gave 54 dilute sun red plants in F_1, *A A b b pl pl* R^g r^r. In F_2 (group 3, table 44) there resulted from a self-pollinated F_1, dilute sun red and green plants in the relation 55:22, a deviation from the expected 3:1 ratio of 2.75 ± 2.56. An F_1 back-crossed with green IVg gave the same two color types in equal numbers, 30 each, exactly as expected. Numerous other crosses of this sort have been observed in connection with studies of the interrelations of aleurone-color and plant-color factors. Since these data are to be presented in a later paper and since they are wholly in accord with the data given in group 3 of table 44, they are not discussed here.

In an earlier section of this paper dealing with the factor pairs *A a*, *B b*, and *Pl pl* only (page 29), it was shown that the green plants there noted are of three kinds, namely, *a b pl*, *a B pl*, and *a b Pl*. Thruout the present section of the paper, which deals with the relation of the multiple-allelomorph series containing R^g, r^r, R^r, r^g, it has been assumed that plants which in the presence of r^r or R^r are dilute purple or dilute sun red, are green in the presence of homozygous R^g. The data presented are wholly in accord with this interpretation, thereby giving considerable assurance of the probable correctness of the hypothesis. The reported interrelations of plant color and aleurone color when the latter was known to involve the *R r* pair, have still further strengthened this assurance. It remains now to present even more direct evidence, namely, that obtained from crosses of green plants encountered in this study, with sun red and dilute sun red plants. These green plants are assumed to be *A b Pl* R^g, type IIIg, and *A b pl* R^g, type IVg.

Certain F_3 and F_4 progenies consisting of green-anthered purples and greens in a 3:1 relation are listed in table 39, group 4. These green plants

were all, presumably, *A b Pl* R^g. Green plants of a later generation, grown from these greens, when crossed with sun red plants, type IIa, gave 64 purple-anthered purples and no other types (table 45, group 1). Another green crossed with dilute sun red resulted in 4 dilute purples. Obviously the same results would have been obtained had the green plants used in these crosses been *a b Pl* r^g, instead of *A b Pl* R^g as they are supposed to have been. As a matter of fact, however, one of these green plants had homozygous colored aleurone, and therefore must have been *A C R*. The other two greens, while they had colorless aleurone, came from lots known, from their 3:1 aleurone-color ratios and from crosses with aleurone testers, to be heterozygous for *C* alone, and therefore *A c R*. Moreover, the green plants from lots consisting of purples and greens in a 3:1 relation could not have been *a a*, for the parents of such lots, if heterozygous for *A*, must have produced purples and browns rather than purples and greens. The green plants could therefore have been nothing other than *A b Pl* R^g.

Similarly, progenies consisting of green-anthered purples and sun reds, and greens, in a 9:3:4 relation, are listed in table 39, group 3. Green plants of these lots and their green descendants might be either *A b Pl* R^g or *A b pl* R^g, or might be heterozygous for *Pl*. Six such green plants were crossed with dilute sun reds (table 45, group 2). None of these greens could have been of the types discussed in the earlier section of this paper, namely, *a b Pl* r^r and the like, for they were shown by appropriate tests (Emerson, 1918) to be *A c R* and some of them have even been used as *C* testers for aleurone color. Two of these green plants crossed with dilute sun reds gave dilute sun reds only, 59 in all, and are consequently regarded as being *A b pl* R^g. Two others by similar crosses gave dilute purples and dilute sun reds in the relation 20:30, a deviation of 5.0 $\pm$2.4 from the expected equality from plants of the genotype *A A b b Pl pl* R^g R^g. Two other greens were crossed with heterozygous dilute sun reds, *A A b b pl pl* R^g r^r, and gave dilute purples, dilute sun reds, and greens in the relation 69:54:106. The theoretical distribution among these three classes for a total of 229 individuals, based on the assumption that the green parent plants were *A A b b Pl pl* R^g R^g, is 57:57:115, a deviation that might occur by chance about once in five trials, P equaling 0.19.

Progenies consisting of dilute purples, dilute sun reds, and greens in a 9:3:4 relation are listed in table 43, group 1A. Descendants of one of

these green plants were crossed with dilute sun reds which were F_1's of crosses between dilute sun red and green IVg. The results were dilute purple and green plants in the relation 328:338 (table 45, group 3), a deviation from a 1:1 ratio of 5.0 ± 8.7. Since the heterozygous dilute sun red plants were *A A b b pl pl* R^g r^r, the green plants crossed with them are assumed to have been *A b Pl* R^g. That this assumption is correct appears the more evident from the fact that the green plants were homozygous for colored aleurone, and hence *A C R*.

Green IVg x *green VIc.*— Twelve crosses between green plants of type IVg and green plants of type VIc gave a total of 159 F_1 plants, all dilute sun red. With respect to aleurone color, all the type IVg plants concerned in these crosses were known to be *A c R*, and, in fact, were in general use as *C* testers for aleurone color. With respect to plant color, therefore, they are assigned the constitution *A b pl* R^g. Of the type VIc greens, four were known to be *A* testers for aleurone color, and were therefore, with respect to aleurone color, *a C R*. Their plant-color constitution is accordingly set down as *a b pl* R^r. Six of the type VIc greens had an aleurone-color constitution of *a C r*, their plant-color genotype being accordingly *a b pl* r^r. The other two VIc greens were certainly *a b pl*, but whether they were R^r or r^r is unknown.

In F_2, dilute sun red and green plants were present in the ratio 420:291 (table 46, group 1, page 154). From an F_1 of the genotype *A a b b pl pl* plus R^g r^r or R^g R^r, a 9:7 ratio of dilute sun red to green is to be expected in F_2, since both *A* and r^r or R^r are assumed to be necessary for the production of anthocyanic pigment, which distinguishes dilute sun red from green. The theoretical ratio for a total of 711 individuals is 400:311. The observed deviation from this ratio, 20.0 ± 8.9, is such as might occur by chance about once in eight trials, P equaling 0.13.

Two F_1 plants backcrossed to green VIc, *a b pl* R^r, gave 66 dilute sun red and 58 green plants, and two backcrosses with green IVg, *A b pl* r^g, gave 96 dilute sun reds and 96 greens, equality of the two classes being expected in the case of both crosses (group 2, table 46).

That the two parent types of green occurred in F_2 is shown by their relations to aleurone and pericarp color. In the case of every cross, green plants were produced from both colored and colorless seeds. Those from colored seeds could have been only *A b pl* R^g. Since some seeds were colorless because of *a a* and some because of *c c*, both parent types of green should have been present in the lots grown from colorless seeds.

In one cross there was present the pericarp factor *P*, which with *A* gives a red and with *a a* a brown pericarp. All the F_2 green plants from colored seeds had red pericarp, and of those from colorless seeds the majority had brown pericarp. From the colorless seeds there should have occurred also a combination type of green, *a b pl* R^g, but no tests were made for the identification of this type.

Ten dilute sun reds of F_2 were tested by their F_3 behavior. Three of these (table 47, group 1) gave dilute sun red and green plants in the relation 108:77, a deviation from a 9:7 ratio of 4.0 ± 4.6. Five other F_2 plants (group 2) gave the two color types in the relation 187:66, a deviation from a 3:1 ratio of 3.0 ± 4.6. Two F_2's (group 3) bred true dilute sun red, producing 78 dilute sun red and no green offspring. Theoretically, of 9 F_2 dilute sun reds, there should occur in F_3, true-breeding, 3:1, and 9:7 progenies in the numerical relation 1:4:4. The observed relation between these three sorts of behavior for the ten F_2's tested was 2:5:3. Deviations such as these might occur by chance about once in two trials, P equaling 0.49.

Green IVg x green VIa.— Certain crosses of green IVg with green VI have given sun red plants in F_1. The type VI greens belonged to families in which the *B* factor was known to be present. They were therefore doubtless *a B pl* plus r^r or R^r, and the F_1's were probably *A a B b pl pl* plus r^r R^g or R^r R^g. F_2 consisted of the three major color types sun red, dilute sun red, and green (table 48, group 1) in the relation 586:161:348. Obviously this is not a 9:3:4 relation, for the deviations from such expectation, −30, −44, +74, could not be expected to occur thru errors of random sampling once in a million such trials, χ^2 equaling 30.9 and P equaling .000000+. As a matter of fact, an F_1 of the genotype suggested above should give in F_2 the three color types observed in the relation 36:9:19. The observed frequencies of the several classes fit this expectation so closely that the deviations from it might occur by chance in about one out of five trials, P equaling 0.19. The comparison of observed and expected frequencies follows:

Color types	Sun red IIa, g	Dilute sun red IVa	Green IVg, VIa, c	Total
Observed	586	161	348	1,095
Calculated	616	154	325	1,095
Difference	−30	+7	+23	0

Not only were the frequencies of the major color types fairly close to expectation, as indicated above, but the expected subclasses of sun red with pink anthers and with green anthers were observed. Counts of anther color were made in the case of only 65 individuals. These plants were distributed to the four color classes, pink-anthered sun red, green-anthered sun red, dilute sun red, and green, in the order 24:9:10:22. The theoretical distribution of 64 individuals being 27:9:9:19, the deviations are such as might occur by chance perhaps twice in three trials, χ^2 equaling 0.91 (when $\chi^2 = 1$ and $n' = 3$, $P = 0.61$).

Only three F_2 sun reds were tested in F_3. One of them (group 2, table 48) bred true sun red, but segregated with respect to anther color. It was therefore presumably *A A B B pl pl* r^r R^g. Two other F_2 sun reds (group 3) gave sun red and green offspring in the ratio 229:71, a deviation of only 4.0 ± 5.1 from a 3:1 ratio. One of these two F_2 plants was crossed with a dilute sun red, resulting in 55 sun red plants. The two F_2 plants, therefore, were presumably *A a B B pl pl*. Anther color was not determined, but the fact that the green plants of F_3 all came from colorless seeds is conclusive evidence for the presence of *A a* and against the presence of r^r R^g. The genotype of the F_2 plants is accordingly set down as *A a B B pl pl* r^r r^r.

Green IIIg x green VIc.— Green plants known to be of type VIc, *a b pl* r^r, were crossed with greens which were known to be R^g R^g and which from their parentage might have had *Pl*. The result in F_1 was dilute purple, supposedly *A a b b Pl pl* r^r R^g. Two F_2 lots (table 49, group 1) consisted of dilute purples, dilute sun reds, and greens in the relation 109:37:135. From the assumed genotype of F_1, there should occur in F_2 the observed color types in the relation 27:9:28. The observed frequencies deviated from the theoretical ones by amounts such as might occur by chance once in three trials, P equaling 0.33. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg, VIb, c	Total
Observed	109	37	135	281
Calculated	119	40	123	282
Difference	—10	—3	+12	—1

The dilute purples of F_2 were presumably all $A\ b\ Pl\ r^r$ and the dilute sun reds all $A\ b\ pl\ r^r$. Of the F_2 greens there should theoretically have been six types, namely, $A\ b\ Pl\ R^g$, $A\ b\ pl\ R^g$, $a\ b\ Pl\ r^r$, $a\ b\ pl\ r^r$, $a\ b\ Pl\ R^g$, and $a\ b\ pl\ R^g$. The relation of these plant colors to aleurone color and to a pericarp color known as cherry, present in these families, affords an opportunity of checking some of these hypothetical formulae. Cherry pericarp is a bright reddish purple, somewhat variable in intensity. In the parent of one of these F_2 progenies it was sufficiently light to make possible the determination of the underlying aleurone color. The F_2 seeds consisted of colored and colorless aleurone in the ratio 140:171, a deviation from a 27:37 ratio of 9.0 ± 5.9, or such a deviation as might occur by chance three times in ten trials, P equaling 0.30. The F_1 plants were known to be $A\ a\ R\ r$, and in order to give a 27:37 ratio with respect to aleurone color they must have been also $C\ c$. Cherry pericarp is of such a nature that it never develops except in the presence of *Pl*. With *A* and *Pl* it is cherry, but with *a* and *Pl* it is brownish. It had been regarded by the writer as due to a factor, *Ch*, but recently Dr. E. G. Anderson has shown (by unpublished data) that the writer's *Ch* is apparently another allelomorph of *R*, and at present it is known to exist only in the form r^{ch}. Since all dilute purples of the lots under consideration here are assumed to be $A\ b\ Pl\ r^{ch}$, they should all have cherry pericarp. Again, since dilute sun reds are *pl pl*, they should all have colorless pericarp. Furthermore, since all green plants from colored seeds are supposed to be $R^g\ R^g$, their pericarp should likewise be colorless. Finally, since the colorless seeds may lack color because of either *a a*, *r r*, or *c c* alone, or because of both *a a* and *r r*, some green plants from colorless seeds should have colorless pericarp, $a\ R^g$ or $A\ c\ R^g$, and some should have brownish pericarp, $a\ Pl\ r^{ch}$. Of course all green plants with *pl pl* also must have colorless pericarp.

The observed results are wholly in accord with these suppositions. In one F_2 progeny, pericarp color was determined for all except a few plants. From seeds with colored aleurone, all the dilute purples had cherry pericarp and all the dilute sun reds and greens had colorless pericarp. These three classes of plant and pericarp color showed frequencies deviating from the theoretical 27:9:18 relation by quantities such as might occur by chance almost once in four trials, P equaling 0.23. From seeds with colorless aleurone, all dilute purples had cherry pericarp, all dilute sun

reds had colorless pericarp, and greens had in part brownish and in part colorless pericarp. The deviations from the expected 27:9:18:20 relation of these four color classes were such as might occur thru errors of random sampling in more than seven out of any ten such trials, P equaling 0.72. The comparisons follow:

Plant color Pericarp color	Dilute purple Cherry IIIa	Dilute sun red Colorless IVa	Green Brownish VIb	Green Colorless IIIg, IVg, VIc	Total
Colored aleurone:					
Observed....	43	10	0	35	88
Calculated...	44	15	0	29	88
Difference...	—1	—5	0	+6	0
Colorless aleurone:					
Observed....	38	11	32	28	109
Calculated...	40	13	27	29	109
Difference...	—2	—2	+5	—1	0

Further tests of the factorial composition, with respect to *Pl*, of some F_2 green plants of this cross are afforded by crosses between them and sun red and dilute sun red plants. One F_2 green crossed with sun red gave 27 purple plants (table 49, group 2). Since the green parent plant came from a colored seed, it is assumed to have been *Pl Pl* R^g R^g plus *A A* or *A a*. Two other greens crossed with dilute sun red gave 39 dilute purple plants, and were therefore *Pl Pl* (group 2, table 49). Since one of these green plants had brownish and the other had colorless pericarp, they are assumed to have been also r^{ch} and R^g R^g, respectively. A fourth F_2 green crossed with sun red gave purple and sun red plants, and a fifth green crossed with dilute sun red gave dilute purple and dilute sun red plants, indicating *Pl pl* (group 3, table 49). The first of these two had brownish and the second had colorless pericarp. They must therefore have been r^{ch} and R^g R^g, respectively. A sixth F_2 green crossed with dilute sun red gave only dilute sun red plants, and so must have been *pl pl* (group 4).

Green IIIg x green VIa.— In the sections immediately preceding this, it has been shown that intercrosses of greens may give dilute sun reds (page 104), dilute purples (page 106), or sun reds (page 105) in F_1, the particular color type depending on the genotypes of the greens chosen for crossing. It remains to be shown that purple Ia can be produced by intercrosses of greens. A cross of green VIa, *a B pl* r^r, with green IIIg, *A b Pl* R^g, should give this result, F_1 being *A a B b Pl pl* R^g r^r. Such a cross has been made, with results as expected.

A stock of green plants was isolated from a cross of brown V, *a B Pl* r^r, with green VIc, *a b pl* r^r, and was shown, by crosses with aleurone testers and with dilute sun red IVa, to be type VIa, *a B pl* r^r. Another lot of greens arose from a cross of purple Ig with green IVg. The purple Ig parent was from a lot consisting of purple Ia, purple Ig, dilute purple IIIa, and green IIIg, coming from a cross of purple Ig with dilute purple IIIa heterozygous for R^g r^r. It was therefore *A A B b Pl Pl* R^g R^g. The green IVg plant with which it was crossed was known to be *A b pl* R^g. The F_1 of this cross consisted, as was expected, of purples and greens only. The purples were type Ig and must have been heterozygous for *B b* and *Pl pl*, and the greens must have been type IIIg and heterozygous for *Pl pl*, or *A A b b Pl pl* R^g R^g. Two of these F_1 greens were crossed with one of the greens of type VIa mentioned above. The two crosses, 9659 and 9660, resulted as expected in purple-anthered purples, type Ia, and pink-anthered sun reds, type IIa, in the relation 18:20. It has been demonstrated, therefore, that by crossing wholly green plants of appropriate genotypes it is possible to produce purple-anthered purples, the most highly colored type known, a type that is dominant to all other types.

Green IIIg x purple Ia.— A green plant with homozygous purple aleurone and belonging to a family (table 39, group 4) consisting of green-anthered purples and greens only, and therefore theoretically being *A b Pl* R^g, was crossed with a purple-anthered purple, *A B Pl* r^r. A purple-anthered purple F_1, *A A B b Pl Pl* r^r R^g, 5350–9, was backcrossed with green IVg of the genotype *A b pl* r^g, with the result that in the next generation there appeared four color types, purple-anthered purple, green-anthered purple, dilute purple, and green, in the relation 28:22:21:29. The deviations from the expected equal distribution of the 100 individuals were such as might occur by chance in considerably more than half of

such trials, P equaling 0.57. It will be recalled that results like these were obtained from a cross of green-anthered purple with dilute purple (page 96), and of course the same results were to be expected since the F_1 in both cases is supposed to have been $A\ A\ B\ b\ Pl\ Pl\ r^r R^g$.

The cross now under consideration has interest from the standpoint of the relation of aleurone color to plant color, and also for certain linkage relations. The F_1 was known to be, with respect to aleurone color, $A\ A\ R\ r$. Whether it was $C\ C$ or $C\ c$ was not known, since a strong red pericarp made aleurone counts impracticable. The green plant on which the F_1 was backcrossed, was determined by appropriate tests to be $C\ C$, so that the relation of the F_1 purple to C is immaterial. The backcross resulted in approximately equal numbers of seeds with and without aleurone color, there being 109 colored and 110 colorless seeds. The colorless seeds must have been $A\ B\ C\ Pl\ r^r\ r^g$ and $A\ b\ C\ Pl\ r^r\ r^g$, and should therefore have produced purple-anthered purples and dilute purples only; while the colored seeds must have been $A\ B\ C\ Pl\ R^g\ r^g$ and $A\ b\ C\ Pl\ R^g\ r^g$, and should correspondingly have produced green-anthered purples and greens only. The results were quite in accord with expectation, as is shown in the following comparison:

Color types	Purple, purple anthers Ia	Purple, green anthers Ig	Dilute purple IIIa	Green IIIg	Total
Colored seeds.....	0	22	0	29	51
Colorless seeds....	28	0	21	0	49

It has been shown earlier in this paper (page 63) that a linkage exists between the factor pair $B\ b$ and a factor pair, $Lg\ lg$, for normal or liguleless leaf, the percentage of crossing-over being about 30. It happens that the F_1 of this cross was $Lg\ lg$ as well as $B\ b$, $B\ lg$ having come from one parent and $b\ Lg$ from the other, and that the green plant used in the backcross was $b\ lg$. There is no question here that the purple-anthered purples and dilute purples produced from colorless seeds differed with respect to the $B\ b$ pair only. Their linkage with liguleless leaf, as indicated by the percentage of crossing-over, was 29.4, or a deviation from 30 of 0.6 ± 2.0. Practically the same linkage relation was found for the plants from colored seeds, green-anthered purples and greens. In this case the percentage of crossing-over was 27.5, a deviation from 30 of

2.5 ± 2.1, or such as might occur by chance about twice in five trials, P equaling 0.42. It is to be assumed, therefore, that the same difference exists between green-anthered purples and greens as between purple-anthered purples and dilute purples, namely, a difference with respect to the factor pair *B b*. This in turn is merely additional evidence that plants which in the presence of r^r are dilute purples, *A b Pl*, appear as greens in the presence of $R^g r^g$, which is the hypothesis under test thruout this section of the paper.

Purple Ia x green-anthered dilute sun red

A purple-anthered purple, known from appropriate aleurone-color tests to be *R R* and hence *A B Pl* R^r, was crossed with a dilute sun red which differed from most dilute sun reds in showing much less anthocyanic pigment, particularly in early stages of growth, than is usual in plants of that type, and in having little, if any, color in its anthers. The F_1's, 2975, were purple-anthered purples. F_2 was expected to show the four color types, purple, sun red, dilute purple, and dilute sun red, commonly found in crosses of purple Ia with dilute sun red IVa. As a matter of fact, the single F_2 progeny grown was found to consist of these four color types as major classes, but each class was found to have colored-anthered (purple or pink) and green-anthered subclasses. The difference between the two subclasses for purple and sun red was sharp, just as is the case in crosses of purple Ia with green IVg, but it was often difficult to separate green-anthered dilute purples from green-anthered dilute sun reds. Ordinarily, anther color (purple or pink) is the surest means of distinguishing between dilute purple and dilute sun red. When both have green anthers the separation must be based on the relative amount of pigment in other plant parts — a difference that is usually not very marked until late in the life of the plants, when dilute purples usually show materially more pigment, especially in parts not exposed to the sun, than do dilute sun reds. It will be recalled that in crosses of purple Ia with green IVg, both colored and green-anthered purples and sun reds appear, but that all the dilute purples and dilute sun reds have colored anthers, the green-anthered individuals appearing as wholly green in all plant parts except perhaps the pericarp. But in the cross here considered, no wholly green plants were found.

The natural supposition is that there is here concerned still another form of the *R* factor, such that, while it does not allow color to develop in the anthers, does nevertheless result in the development of some anthocyanic pigment in other parts of the plant. The dilute sun red plant used as one parent of this cross was found to be *A c R* with respect to aleurone. The factor particularly concerned in the behavior here reported is therefore assigned the designation R^{rg}. The F_1 plants are accordingly assumed to have been *A A B b Pl pl* R^r R^{rg}. The frequency distribution for the eight color types observed in F_2 approached the theoretical distribution so closely that deviations of the magnitude observed might occur by chance nearly three times in any ten such trials, P equaling 0.72. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute purple	Dilute sun red	Dilute sun red	Total
Anther color	Purple	Green	Pink	Green	Purple	Green	Pink	Green	
Observed...	212	77	66	22	66	23	22	3	491
Calculated.	207	69	69	23	69	23	23	8	491
Difference..	+5	+8	−3	−1	−3	0	−1	−5	0

One F_2, a green-anthered purple, was tested in F_3. This plant bred true, producing 128 green-anthered purples and no other types.

It is unfortunate that the relation of aleurone color to plant color in this cross afforded no check on the assumption that the observed behavior with respect to anther color of dilute purples and reds was due to a factor belonging to the allelomorphic series R^r, R^g, r^r, r^g. True, the F_1 plant tested was heterozygous with respect to aleurone color, but this was known to be due to *C c*. Since no further tests have been made, the only evidence in support of the assumption of a factor R^{rg} is the very close fit of observed with theoretical frequency distributions, the fact that colored and green anthers in purple and sun red types of many other crosses have been found to be due to the *R* factor, and the demonstrated presence of *R* in the green-anthered sun red plant used in the cross.

Summary of results involving the allelomorphic series R^r, R^g, R^{rg}, r^r, r^g, r^{ch}

Crosses of brown with green of type IVg have been shown to result in purple F_1's, and in eight color types in F_2 in a numerical relation approximating 81:27:27:9:27:9:36:40, or in six major color types, anther color being disregarded, in approximately the relation 108:36:27:9:36:40.

It has been noted that these results are wholly unlike those for crosses of brown with green reported in an earlier section of this paper, and are similar in general, tho with marked differences in detail, to previously discussed crosses of brown with dilute sun red. As an interpretation of these results, it has been assumed that, in addition to the three pairs *A a*, *B b*, *Pl pl*, a fourth pair — members of a multiple-allelomorph series, such as $R^r R^g$, $r^r R^g$, or $R^r r^g$ — is concerned. It has been assumed further that R^r or r^r is necessary ordinarily for the development of dilute purple and dilute sun red and for the appearance of purple and pink anthers in purples and sun reds, respectively, while $R^g R^g$ or $r^g r^g$ is necessary for green anthers of purples and sun reds and for the conversion of dilute purples and dilute sun reds into wholly green plants. Similarly, the appearance of green-anthered dilute purples and dilute sun reds in a single cross has been ascribed to $R^{rg} R^{rg}$. The relation of the *R* allelomorph to both aleurone color and plant color has afforded reliable tests of the hypothesis. Other tests have consisted of the behavior in later generations of the several F_2 color types and the results of intercrosses between these types. Neither of these tests has been carried to the point of exhausting all the possibilities, but in all a considerable number of tests have been made and all have given results in support of the hypothesis. A single linkage test, involving the *B b* pair with leaf type, *Lg lg*, has afforded added support. On the whole, therefore, the hypothesis has been, if not substantiated, at least rendered highly probable.

RELATION OF ALEURONE FACTORS *C c* AND *Pr pr* TO PLANT COLOR

The relations of the aleurone factors *A* and *R* to plant color have been noted repeatedly in this account. A single observation suggests a relation between the aleurone-factor pair *C c* and leaf color. Culture 2909 came from colored seeds of a selfed ear showing a 3:1 ratio of colored to white seeds, and therefore heterozygous for a single pair of aleurone-color factors. Several ears in the resulting progeny also gave 3:1 ratios. Tests of four plants with aleurone testers gave conclusive evidence that the *C c* pair was the one concerned. One selfed plant of the lot, 2909–32, had 318 colored and 105 white seeds. Both the colored and the white seeds produced only sun red plants, some with green and some with pink anthers, indicating the genotype *A A B B C c pl pl* $R^r R^g$. All the plants showed strong sun red pigment in the sheaths and the outer husks, but

there was distinctly more red color in the leaves of the plants from colored seeds than in the leaves of the plants from white seeds. Particular attention has not been given to a possible effect of the *C* factor on mature plant colors of other color types. Many cultures of dilute sun reds and greens have afforded opportunities for observing any effect of *C* and *c* on red color in the leaves of seedlings, but no effects have been noted. No particular attention was paid to the matter at the time when the seedlings were under observation, but if the *C c* pair had exerted any marked influence it would probably have been noted.

Numerous cultures of dilute sun red seedlings have been noted with respect to possible effects of the aleurone-factor pair *Pr pr*, but no effect has been observed, the purple and the red seeds having produced seedlings with apparently the same intensity of red color. Likewise, no influence of *Pr pr* on mature plant color has ever been observed in the case of either sun red or dilute sun red. With purple and dilute purple plants, however, a distinct effect is noticeable. Purple and dilute purple plants from seeds with purple aleurone have purple anthers, while those from seeds with red aleurone have reddish purple anthers (Plate I, 1 and 3, and Plate II, 1 and 3). A similar effect is often seen also in the color of the inner husks. In neither the anthers nor the husks is the effect always sufficiently distinct to make possible an accurate separation of plants from purple and from red seeds if they are growing in mixed cultures. In some cases, however, the difference is very distinct. And when the seeds are separated with respect to purple and red aleurone, the two lots of plants resulting usually show fairly distinct differences in anther color and often in husk color as well.

EXPRESSION OF PLANT-COLOR AND ALEURONE-COLOR FACTORS

The mode of expression of the several plant-color factors has been discussed in detail in this paper, and similar discussions of aleurone-color factors are available in numerous other papers. Since aleurone colors and certain plant colors — the purple-red series — are doubtless anthocyanins, it seems natural to expect close interrelations between them. Many such relations have been noted in this account. There are certain matters, however, which need to be brought together in a summary discussion.

It will be recalled (Emerson, 1918) that for the development of any aleurone color, the presence of three dominant factors, *A*, *C*, and *R*, and also of a duplex recessive factor pair, *i i*, is necessary. The *Pr pr* pair has no visible expression except when associated with this combination of the other factors, and then it determines whether the color shall be purple or red. So far as is now known, the plant-color situation with respect to complementary factors is not quite so complex. Something of the same sort is seen, however, in the fact that no anthocyanic pigment ordinarily develops except either in the presence of *A* and R^r, r^r, or r^{ch}, or in the presence of *A*, *B*, and R^g R^g or r^g r^g. With the first of these combinations, the pairs *B b* and *Pl pl* determine the particular color type of the purple-red series. Two of these types, purple and dilute purple, are modified further by *Pr pr*, and the intensity of their color depends also on the member of the *R* series present, r^{ch} exerting a more pronounced effect than R^r or r^r. One type at least, sun red, is influenced somewhat by *C c*. With the second combination, *A*, *B*, and R^g R^g or r^g r^g, the pair *Pl pl* determines whether the type shall be purple or sun red. For the formation of the non-anthocyanic (flavonol) pigment, brown, the interaction of *a a* with either *B* or *Pl* is essential, and usually very little color develops except when both *B* and *Pl* are present. Brown is made more intense by the presence of r^{ch}.

Of the factors concerned with plant colors of maize, the *A a* pair is one of the most fundamental, since it differentiates sharply the anthocyanins of the purple-red series, *A B Pl*, *A B pl*, *A b Pl*, *A b pl*, from the non-anthocyanic brown, *a B Pl*, and the slightly brown or green *a B pl* and *a b Pl* and the wholly green *a b pl*. Without *A* no anthocyanin shows in either the aleurone or the other parts of the plant. A second fundamental pair is *Pl pl*, which differentiates the sun colors from those that develop in local darkness. Purple (*A B Pl*), dilute purple (*A b Pl*), and brown (*a B Pl*) are all able to develop in darkness; while sun red (*A B pl*), dilute sun red (*A b pl*), and the slight brown sometimes seen in *a B pl*, do not develop except in the presence of light. Whether or not the slight brown sometimes present in *a b Pl* forms in darkness has not been determined. To the *Pr pr* pair is due a definite qualitative difference in the colors formed which is presumably associated with a difference in chemical composition of the pigments. In the presence of *Pr* aleurone color is purple, and with *pr* it is red, and a similar difference, tho not always

so sharp a one, is seen in the effects of *Pr pr* on the anther and husk color of purples and dilute purples. The factors R^g and r^g on the one hand, both recessive with respect to plant color, and R^r and r^r on the other hand, both dominant for plant color, apparently always differentiate between colored and colorless anthers and silks in the purple-red series of plant colors, and, when *B* is absent, determine whether or not anthocyanin forms in any part of the plant. The pair *B b* influences mainly the intensity of pigmentation. Thus, purple, *A B Pl*, is more strongly colored than is weak purple, $A\ B^w\ Pl$, which in turn is more strongly colored than is dilute purple, *A b Pl*. The same relation holds between sun red, *A B pl*, weak sun red, $A\ B^w\ pl$, and dilute sun red, *A b pl*. Brown color shows very little in *a b Pl* but is strongly developed in *a B Pl*. A similar difference, however, exists between the slight brown of *a B pl* and the full brown of *a B Pl*. In the one case in which an effect of *C c* has been noted, *C* acted as an intensifier of color.

There are somewhat marked differences between the several factor pairs with respect to the stage of plant development at which their influence is expressed. Seedlings of purple, sun red, dilute purple, and dilute sun red normally exhibit no characteristic differences in intensity or extent of pigmentation. The *B b* and *Pl pl* pairs, which differentiate these color types so sharply at a later stage of growth, do not, therefore, come into expression early. All of these types are more highly colored late in their growth period than they are as seedlings, but the later changes are much more pronounced, for instance, in dilute purple than in dilute sun red, and somewhat more so in purple than in sun red. Apparently, *Pl* exerts its influence comparatively late, but under the intensifying influence of *B*, even *Pl* expresses itself fairly early.

The several factor pairs differ more or less with respect to the particular plant parts affected. Differences in the expression of *B*, B^w, and *b* are more apparent in the husks and the sheaths, particularly the upper sheaths, than elsewhere. When plants of the genotype *a B pl*, commonly classed as green, show any brown, the color is limited to the sheaths and the outer husks. The difference between purple (*A B Pl*) and sun red (*A B pl*) on the one hand, and dilute purple (*A b Pl*) and dilute sun red (*A b pl*) on the other, is more pronounced in the husks and the sheaths than elsewhere. Little difference is apparent between the two groups with respect to the color of anthers, glumes, silks, and the like. The pair

Pl pl is perhaps expressed most definitely in the color of anthers, tho the expression is by no means limited to them. Purple (*A B Pl*) and dilute purple (*A b Pl*) differ from sun red (*A B pl*) and dilute sun red (*A b pl*), not merely in having purple rather than pink anthers, but also in the coloration of their inner husks, their culms, and the like. What little brown color is seen in *a b Pl* is limited almost wholly to the staminate inflorescence. The staminate inflorescence of purples, *A B Pl*, and of browns, *a B Pl*, is strongly colored, but that of dilute purple, *A b Pl*, except for anther color, is not very different from what is seen in dilute sun red, *A b pl*. The *Pl* factor, when associated with r^{ch}, is expressed in the pericarp as cherry in purple and in dilute purple, and as brownish in brown and in green of the genotype *a b Pl*.

Factors *B b* and *Pl pl* are not known to be concerned with aleurone color. All the other factors affecting plant color are aleurone-color factors also. Of these the pair *Pr pr* influences anther color of purple and dilute purple, and to some degree the husk color as well. The pair *C c* has been observed to affect the leaf color of mature plants of the sun red type. The pair *A a* is expressed to some degree in all such parts as culms, sheaths, husks, glumes, anthers, and silks. The pericarp, if a pericarp factor *P* is present, is red with *A* and brown with *a*, or if r^{ch} and *Pl* are present, it is cherry with *A* and brownish with *a*. The *R* series of factors influences many plant parts. With duplex R^g or r^g, no color develops in any part of the plant, except the aleurone, provided *B* is absent. With *B* these factors give colorless anthers and silks merely. Factors R^r and r^r, if *A* also is present, affect practically all plant parts in which anthocyanic pigments ever develop, but are not known to have any influence on the color of the pericarp. The factor r^{ch} is, however, concerned with pericarp color provided *Pl* also is present. This factor has a marked influence on the amount of color that forms in the leaves, particularly of dilute purple and dilute sun red.

It is of no little interest that the *R* series of factors, which behaves as a group of multiple allelomorphs with regard to plant color, usually acts as a simple pair in respect to aleurone color.[6] Moreover, some of these factors act as dominants with respect to aleurone color and as recessives with respect to plant color, while the dominance of others is

[6] There is some evidence that at least one aleurone-color pattern is dependent on an allelomorph of *R r*, the three thus constituting a group of triple allelomorphs affecting aleurone-color development.

the reverse of this. For example, r^r and r^{ch} are recessive for aleurone and dominant for plant color, and R^g is dominant for aleurone and recessive for plant color, while R^r is dominant and r^g recessive for both aleurone and plant colors.

SUMMARY

In this account, six major plant-color types of maize, purple, sun red, dilute purple, dilute sun red, brown, and green (colorless), together with the subtypes, weak purple, weak sun red, green-anthered purple, green-anthered sun red, and five genotypes of green, are described and illustrated, and their environmental and genetic relations are discussed.

The sun red and dilute sun red types are shown to be dependent on light for the development of their color, while the purple, dilute purple, and brown types develop their characteristic colors in darkness. Diversities of temperature and of soil moisture are shown to have no direct effect on the formation of maize plant colors but to have an indirect relation to them thru their influence on soil fertility, which in turn bears a definite relation to the development of the purple-red series of plant color, anthocyanins, but little or no relation to brown. Sun colors particularly are shown to be markedly intensified by infertile soil. It is noted that the several types of the purple-red series are sharply differentiated when grown on fertile soil, but that their characteristic differences are largely masked by growth on infertile soil, while the brown-green series is most readily distinguished from the purple-red series, especially in the seedling stage, if grown on infertile soil. It is suggested that the effect of infertile soil may be due to a deficiency of nitrogen, and perhaps of phosphorus. Observations indicating a close connection between the accumulation of carbohydrates and strong coloration are reported, and the inference that the effect of infertile soil is brought about thru checking growth without inhibiting photosynthesis, thus allowing an accumulation of carbohydrates, is discussed.

In an attempt at a genetic analysis of the several plant-color types, data accumulated during a period of some ten years, and involving an examination of approximately 680 progenies and not less than 48,000 individual plants, are reported. As an interpretation of the results obtained from the more complex crosses, the allelomorphic pairs *A a* and *Pl pl*, and the multiple allelomorphs B, B^w, b^s, b, and R^r, R^g, R^{rg},

r^r, r^g, r^{ch}, are assumed and genetic formulae are assigned to the several color types as follows: purple, *A B Pl*; sun red, *A B pl*; dilute purple, *A b Pl*; dilute sun red, *A b pl*; brown, *a B Pl*; green, *a B pl*, *a b Pl*, *a b pl*; all these having in addition R^r, r^r, or r^{ch}. The factor R^{rg} is assumed to be the causal factor for green anthers and silks in purple, sun red, dilute purple, and dilute sun red types, and R^g and r^g are assumed to have the same effect on purple and sun red and to insure colorlessness (green type) thruout in what would otherwise be dilute purple and dilute sun red, the *R* series having no effect on brown, except for r^{ch}, which intensifies brown as well as purple and dilute purple. Of the *R* series, R^r is dominant and r^g is recessive for both plant and aleurone color, r^r and r^{ch} are dominant for plant and recessive for aleurone color, R^g is recessive for plant and dominant for aleurone color, and R^{rg} is dominant for aleurone color and also for plant color except of the anthers and the silks, for which it is recessive. The *A a* pair is concerned with both aleurone and plant color, and the aleurone pairs *C c* and *Pr pr* are assumed to exert a modifying effect on certain plant colors.

The principal hypotheses involved are shown to be in keeping with observed facts when subjected to practically all the available genetic tests, such as backcrosses of F_1 with multiple recessives, behavior of F_2 types in later generations, intercrosses of the several F_2 types, relation of aleurone color to plant color, linkage of certain plant-color types with normal- and liguleless-leaf types and of other plant-color types with yellow and white endosperm. Approximately 32 per cent of crossing-over is reported between *B b* and *Lg lg* and about 20 to 30 per cent between *Pl pl* and *Y y*.

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APPENDIX

TABLE 1. F_1 PROGENIES OF PURPLE Ia x GREEN VIc

Pedigree nos.		Number of F_1 plants (Purple Ia)
P_1	F_1	
724–1 x 722–1	857	18
1121–8 x 1122–7	1420, 1512, 2022	40
1122–5 x 1121–2	1419, 1511	36
1525–5 x 1546–5	2056	17
Total, 4 progenies		111

TABLE 2. F_2 PROGENIES OF PURPLE Ia x GREEN VIc

Group	Pedigree nos.		Number of F_2 plants					
	F_1	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
1	1419– 1..	1513.....	94	22	26	12	20	23
	1511– 1..	2018.....	61	19	13	4	13	9
	1512–12..	2020.....	54	16	23	7	21	7
	2022– 3..	4012, 4013.	7	6	6	3	4	1
	2056– 6..	2415, 2416, 4284.....	39	13	17	4	16	10
	–11..	2417, 2418, 2553–2559, 4001–4007.	96	22	24	3	26	8
	–16..	2412, 4066, 4067.....	17	3	11	1	8	7
	Total, 7 progenies.....		368	101	120	34	108	65
2	1514–24..	2054.....	20	7	8	1	5	2
	–31..	2055.....	22	4	4	2	2	6
	2000– 8..	2419, 4065.	92	29	21	8	19	25
	2019–28..	4281.....	24	8	4	2	4	6
	–34..	4282.....	21	6	4	4	7	4
	2906– 1..	5303.....	17	7	5	2	6	3
	2907– 1..	5290–5293, 7050, 7051	93	26	34	7	34	23
	– 7..	5299, 5300, 7054, 7055	105	46	30	10	38	31
	2981– 2..	5056, 5067.	17	4	5	1	8	3
	– 5..	5068, 5069.	20	6	2	1	2	3
	4020– 7..	5712, 6810.	109	44	26	12	31	33
	4032– 1..	5739.....	16	5	3	2	3	2
	– 3..	5084.....	15	7	5	4	4	3
	– 4..	5087.....	13	5	4	1	7	7
	Total, 14 progenies....		584	204	155	57	170	151
	Total, 21 progenies....		952	305	275	91	278	216

TABLE 3. F_2 PROGENIES OF PURPLE x GREEN BACKCROSSED WITH GREEN (Ia x VIc) x VIc

Group	Pedigree nos.		Number of F_2 plants					
	F_1 x VIc	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
1	1420– 1 x 1430– 3	1514	12	19	15	16	14	45
	1511– 1 x 1516– 1	2019	18	8	12	8	18	50
	1512–12 x –14	2021	23	18	16	10	13	44
	2056–16 x 1995– 6	2413, 4068	4	10	8	6	8	18
	Total, 4 progenies		57	55	51	40	53	157
2	2867–69 x 4032– 1	5740	7	4	6	3	4	10
	2906– 1 x 2887–10	5305	7	5	2	8	3	9
	2907– 1 x –22	5296, 7052, 7053	10	11	10	11	9	26
	– 7 x 4032–41	5301, 5302	16	16	16	19	25	47
	4020– 7 x 2888–13	5714	2	9	9	4	4	18
	4032– 2 x 2921– 4	5094	8	6	18	12	15	33
	3 x 2888– 5	5086	19	16	21	12	18	46
	3 x 2922–16	5085	14	10	22	16	8	34
	4 x 2888– 1	5089	5	15	12	17	18	45
	4 x 2921– 4	5090–5092	25	13	19	18	15	54
	Total, 10 progenies		113	105	125	120	119	322
	Total, 14 progenies		170	160	176	160	172	479

TABLE 4. F_1 PROGENIES OF DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_1 plants			
	P_1	F_1	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2025–23 x 2192–14..	2333, 4314.....	25	.....	.....	.....
	2029– 8 x 1945–11..	2304, 3596.....	30	.....	.....	.....
	– 8 x 2013–19..	2311.....	17	.....	.....	.....
	– 8 x 2014– 8..	2310, 4034.....	5	.....	.....	.....
	2031–10 x 1945–10..	2309.....	16	.....	.....	.....
	–32 x 2012– 1..	2322.....	20	.....	.....	.....
	2948–16 x 4042– 2..	5168, A108, A120....	79	.....	.....	.....
	4253– 2 x 4299– 2..	5528, 6748A.....	46	.....	.....	1
	4305– 5 x 4042– 2..	5193, 5194.....	24	.....	.....	.....
	Total, 9 progenies.....		262	.....	.....	1
2	2018–69 x 2192–18..	2386, 4301.....	30	35	.....	.....
	2030–13 x –14..	4319.....	7	6	.....	.....
	2031–20 x 2012– 1..	2325, 2326, 2543, 2544, 2950, 2951..	55	55	.....	.....
	2043– 2 x 2026–17..	2347, 4326.....	15	18	.....	.....
	2049–14 x 2192–14..	2336, 4327.....	24	21	.....	.....
	2473– 3 x 2341– 1..	4029.....	4	2	.....	.....
	4370– 5 x 3000– 2..	4746, 4747.....	8	10	.....	.....
	Total, 7 progenies.....		143	147	.....	.....
3	2023–19 x 2192–12..	2332, 4311.....	19	.....	26	.....
	–23 x –12..	2330, 4310.....	15	.....	16	.....
	2027– 9 x –14..	2334, 4316.....	15	.....	18	.....
	2410– 4 x 2417– 2..	2993, 2994.....	9	.....	6	.....
	– 6 x – 1..	2995–2998.....	23	.....	32	.....
	5500– 5 x 5130– 1..	A65.....	24	.....	25	.....
	Total, 6 progenies.....		105	.....	123	.....
4	2025–10 x 2192–14..	4315.....	1	2	6	3
	2029–27 x 2012– 1..	2319, 4055.....	4	3	5	5
	–32 x – 1..	2316, 4318.....	3	5	6	3
	–34 x 2014– 8..	2314, 4054.....	1	1	2	6
	Total, 4 progenies.....		9	11	19	17

TABLE 5. F_2 PROGENIES OF DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_2 plants					
	F_1	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
1	2310– 2..	4036, 4037.	15	7	6	3	3	7
	2332– 1..	2999, 3000.	31	9	8	1	15	7
	2950– 1..	5036, 5037.	36	12	12	2	10	9
	– 4..	5030, 5031.	37	15	13	3	8	13
	–17..	5034, 5035.	32	5	14	6	13	9
	–19..	5032, 5033.	39	12	10	3	12	5
	2995– 7..	5000–5007.	75	24	20	5	21	17
	2996– 1..	5008, 5009.	150	50	58	20	48	45
	4029– 2..	5095.....	61	23	11	5	22	11
	4034– 1..	5098, 5099.	46	12	19	7	17	7
	– 2..	5104.....	42	20	17	8	13	21
	5193– 1..	A135.....	20	5	4	3	4	1
	5194– 5..	A136.....	10	3	12	1	4	7
	5528– 8..	6748B.....	49	11	14	4	12	18
	Total, 14 progenies....		643	208	218	71	202	177
2	2973– 5..	5056–5062.	55	23	21	6	17	17
	2974– 9..	5063–5065.	75	24	23	10	18	22
	4046– 3..	5157, 5158.	20	11	6	5	7	4
	5173– 4..	A128.....	19	5	8	1	9	9
	S17–19...	7762.....	35	11	5	1	14	4
	Total, 5 progenies		204	74	63	23	65	56
	Total, 19 progenies....		847	282	281	94	267	233

TABLE 6. F_2 PROGENIES OF DILUTE SUN RED x BROWN BACKCROSSED WITH GREEN (IVa x V) x VIc

Pedigree nos.		Number of F_2 plants					
F_1 x VIc	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
2310– 1 x 2411– 6..	4035.....	3	4	3	6	2	17
2922–13 x 4029– 2..	5652, 5653..	22	13	19	24	27	75
4029– 2 x 2921–10..	5096.....	9	18	12	8	13	51
4034– 1 x 2922–16..	5100–5103..	10	13	17	11	9	33
– 2 x 2921–68..	5105.....	12	5	5	4	4	16
5813–25 x 5528– 8..	6749.....	3	0	2	4	1	9
A129–12 x A108– 6..	A243, A244.	25	19	20	15	23	48
To al, 7 progenies.....		84	72	78	72	79	249

TABLE 7. F_2 PROGENIES OF PURPLE x GREEN AND DILUTE SUN RED x BROWN BACKCROSSED WITH DILUTE SUN RED

(Ia x VIc) x IVa, AND (IVa x V) x IVa

oup	Pedigree nos.		Number of F_2 plants			
	F_1 x IVa	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2056–16 x 1992–13.....	2414, 4069, 4070...	18	16	21	15
	2889–54 x 4032– 1.....	5741–5744.....	24	27	21	24
	Total, 2 progenies.....		42	43	42	39
2	6730 – 9 x 6748A– 5..	7467, 7828.....	87	79	75	71
	6748A–16 x 6751 –22..	7229.....	40	32	42	41
	–18 x –22..	7230.....	28	28	26	35
	–19 x – 1..	7231.....	40	33	30	36
	–20 x – 1..	7232.....	30	25	32	20
	A121– 6 x A108– 8..	A241, A242, A461, A462.....	28	25	38	45
	L188– 1 x 5528 – 8..	6786, S2.....	4	5	3	4
	Total, 7 progenies.....		257	227	246	252
	Total, 9 progenies.....		299	270	288	291

TABLE 8. F_3 PROGENIES OF SELFED AND BACKCROSSED F_2 PURPLE PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

oup	Pedigree nos.		Number of F_3 plants					
	F_2	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green
	1513–41.....	2045, 4008, 4009.....	32	14	8	3	6	(VIa,b,c) 8
	–68.....	2048, 2475, 4010, 4011	61	14	21	7	18	10
1	2018– 2.....	4268.....	15	7	5	0	6	4
	– 9.....	4271.....	13	8	6	1	3	3
	2020– 1.....	4275.....	16	8	6	2	7	3
	4065– 6.....	5210.....	9	3	3	0	1	1
	–62.....	5213.....	25	7	6	2	4	1
	–63.....	5214.....	22	5	5	1	12	4
	Total, 8 progenies.....		193	66	60	16	57	34
	2020-117 x 2043-11	4279.....	4	4	11	4	4	18

TABLE 8 (*continued*)

Group	Pedigree nos.		Number of F_3 plants					
	F_2	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green
2	1513 – 35	2046	11	4	6	1	.....	.....
	–138	2052	16	6	1	2	.....	.....
	2018 – 6	4270	25	9	5	5	.....	.....
	4066 – 3	5216, 5217	38	14	13	5	.....	.....
	6748B– 41	7400	12	3	4	0	.....	.....
	Total, 5 progenies		102	36	29	13	.....	.....
								(VIa)
3	1513– 59	2047	20	6	.....	.....	5	3
	– 92	2053	24	6	.....	.....	3	3
	–133	2049	16	4	.....	.....	9	2
	4037– 5	5136, 5137	35	15	.....	.....	6	7
	Total, 4 progenies		95	31	.....	.....	23	15
	2020–46 x 2200– 8	4283	5	1	.....	.....	3	3
	2411– 4 x 2412– 2	2981–2983	8	6	.....	.....	2	10
	2443– 2 x – 2	2984–2986	7	8	.....	.....	7	4
	2922–12 x 4037– 5	5138–5140	34	43	.....	.....	32	36
	Total, 4 progenies		54	58	.....	.....	44	53
								(VIb)
4	2018–27	4280	19	.....	5	.....	9	1
	2020–15	4276	19	.....	3	.....	9	3
	–30	4277	29	.....	7	.....	6	4
	4001–12	5079	11	.....	4	.....	4	1
	4005– 5	5010–5013	195	.....	77	.....	71	29
	4066– 5	5218	29	.....	12	.....	6	3
	5099–22	A78	16	.....	6	.....	6	1
	Total, 7 progenies		318	.....	114	.....	111	42
5	1513– 2	2050	19	3	.....	.....	.....	.....
	–110	2051	16	6	.....	.....	.....	.....
	2018– 92	4273	31	13	.....	.....	.....	.....
	–119	4269	33	9	.....	.....	.....	.....
	2412– 1	4033	40	13	.....	.....	.....	.....
	Total, 5 progenies		139	44	.....	.....	.....	.....

TABLE 8 (*concluded*)

Group	Pedigree nos.		Number of F_3 plants					
	F_2	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green
5 (*continued*)	2411–5 x 2412–1	4032	4	1	.....	.....	.....	.....
	2434–1 x –1	4019, 4020	8	8	.....	.....	.....	.....
	Total, 2 progenies		12	9	.....	.....	.....	.....
6	4006– 1	5014, 5015	126	.....	37	.....	.....	.....
	4065–14	5209	42	.....	12	.....	.....	.....
	Total, 2 progenies		168	.....	49	.....	.....	.....

TABLE 9. F_4 PROGENIES OF SELF-POLLINATED PURPLE PLANTS OF F_3 LOTS CONSISTING OF COLOR TYPES Ia, IIIa, V, AND VIb

Group	Pedigree nos.		Number of F_4 plants			
	F_3	F_4	Purple Ia	Dilute purple IIIa	Brown V	Green VIb
1	5010– 7	7020, 7021	51	15	12	8
	– 9	7022, 7023	53	19	22	6
	–11	7024, 7025	46	17	26	5
	5011– 4	7028, 7029	35	17	14	1
	Total, 4 progenies		185	68	74	20
2	4276–32	5181, A170	46	12	.....	.....
	5010– 2	7092	14	2	.....	.....
	5011– 6	7091, 6837	28	14	.....	.....
	Total, 3 progenies		88	28	.....	.....
3	5011–2	7026, 7027	67	.....	21	.....

TABLE 10. F_3 PROGENIES OF F_2 SUN RED PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants		
	F_2	F_3	Sun red IIa	Dilute sun red IVa	Green
					(VIa, c)
1	1513–152	2038, 2474, 4292	38	11	11
	2018– 4	4286	19	7	*16
	– 39	4287	30	12	11
	– 44	4288	9	4	6
	– 56	4289	30	8	11
	Total, 5 progenies		126	42	55
	1513–100 x 1516–20	2039, 4293	7	8	†23
	2018– 56 x 2043–11	4290	3	1	7
	2020–118 x –11	4291	4	9	20
	Total, 3 progenies		14	18	50
2	4037–2	5126, 5127	23	9	.....
3	4037–24 x 2921–15	5128, 5129, 7074	50	.....	(VIa) 43

* Plus one brown V plant.
† Plus one purple Ia plant.

TABLE 11. F_3 PROGENIES OF F_2 DILUTE PURPLE PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants		
	F_2	F_3	Dilute purple IIIa	Dilute sun red IVa	Green
					(VIb, c)
	2018–18	4296	14	6	12
	4037– 9	5117, 5118	38	9	16
	5099– 7	A77	35	15	19
1	A120– 13	A229	8	1	3
	Total, 4 progenies		95	31	50
	2922–16 x 4037–9	5119–5121	21	25	57
2	4066–9	5219	57	21	.....
					(VIb)
	4037–14	5122, 5123	16	.....	5
3	5095–29	A63	9	.....	1
	5290–12	7056, 7057	60	.....	14
	Total, 3 progenies		85	.....	20
4	4065–50	5212	21	.....	.....

TABLE 12. F_3 PROGENIES OF F_2 DILUTE SUN RED PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Dilute sun red IVa	Green VIc
	4036–9	5115	16	6
	6750–4	7247, 7399	34	8
1	A120–8	A228	12	3
	Total, 3 progenies		62	17
	4036–8	5116	27	.....
	4042–2	5166	65	.....
2	Total, 2 progenies		92	.....
	2922–18 x 4042–2	5169–5171	69	.....

TABLE 13. F_3 PROGENIES OF F_2 BROWN PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Brown V	Green
				(VIa, b, c)
1	1513–12	2025, 4313	33	35
	2020– 8	4309	16	13
	–47	4305	23	*11
	–98	4307	16	8
	4065–12	5211	8	7
	Total, 5 progenies		96	74
				(VIa, b)
2	1513– 16	2030	21	6
	– 39	2026	23	10
	–143	2027	30	9
	–194	2023	32	9
	2018– 69	2539, 2540, 4299, 4300	94	25
	– 96	2338, 4302	64	20
	2020– 57	4306	29	9
	4037– 6	5130, 7076	46	12
	6748B–37	7401	15	4
	Total, 9 progenies		354	104
	4037–6 x 2922–6	5131–5133	34	41

* Plus one sun red IIa plant.

TABLE 14. PROGENIES OF F_2 AND F_3 BROWN PLANTS, OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V, CROSSED WITH DILUTE SUN RED IVa PLANTS

Group	Pedigree nos.		Number of F_3 plants			
	F_2 x IVa	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2018–69 x 2192–18..	2386, 4301.....	30	35	.....	.....
	4370– 5 x 3000– 2..	4746, 4747.....	8	10	.....	.....
	Total, 2 progenies.....		38	45	.....	.....
2	2410–4 x 2417–2....	2993, 2994.....	9	.....	6	.....
	–6 x –1....	2995–2998.....	23	.....	32	.....
	Total, 2 progenies.....		32	.....	38	.....
3	5095–20 x L170–1 ..	S17.....	15	.....	.....	.....
	F_3 x IVa	F_4	Number of F_4 plants			
4	2025–10 x 2192–14..	4315.....	1	2	6	3
5	2030–13 x 2192–14..	4319.....	7	6	.....	.....
	2043– 2 x 2026–17..	2347, 4326.....	15	18	.....	.....
	Total, 2 progenies.....		22	24	.....	.....
6	2023–19 x 2192–12..	2332, 4311.....	19	.....	26	.....
	–23 x –12..	2330, 4310.....	15	.....	16	.....
	2027– 9 x –14..	2334, 4316.....	15	.....	18	.....
	5500– 5 x 5130– 1..	A65.....	24	.....	25	.....
	Total, 4 progenies.....		73	.....	85	.....
7	2025–23 x 2192–14..	2333, 4314.....	25	.....	.....	.....
	4253– 2 x 4299– 2..	5528, 6748A.....	*46	.....	.....	.....
	4305– 5 x 4042– 2..	5193, 5194.....	24	.....	.....	.....
	Total, 3 progenies.....		95	.....	.....	.....

* Plus one dilute sun red IVa plant.

TABLE 15. F_3 PROGENIES OF SELFED AND BACKCROSSED GREEN PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree Nos.		Number of F_3 plants (Green)
	F_2	F_3	
			(VI)
1	1513 – 42	2033	22
	–106	2036	18
	–111	2032	13
	4036 – 6	5114	22
	4037 – 29	5124, 5125	42
	4066 – 4	5215	32
	5095 – 30	A62	8
	6748B– 11	7402	22
	Total, 8 progenies		179
2	1514– 9	2034	20
	–37	2035	19
	–47	2037	18
	6749– 1	7242	19
	– 4	7243	20
	Total, 5 progenies		96
			(VIa)
3	2019– 40	2364, 4356	*26
	– 63	2356, 4355	24
	– 92	2384	10
	– 98	2374	10
	–106	2357	15
	Total, 5 progenies		85
			(VIb)
4	2019–33	2349, 4354	29
	–57	2373, 4353	34
	–73	2379	10
	–84	2383	14
	Total, 4 progenies		87
			(VIc)
5	2019–17	2395	14
	–25	2348, 4357	29
	Total, 2 progenies		43

* Plus one brown V plant.

TABLE 16. F_1 PROGENIES OF CROSSES OF GREEN VIa, VIb, AND VIc WITH DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_1 plants		
	P_1	F_1	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2047–25 x 2192–14	2392	16	.....	.....
	2049–12 x –14	2393	20	.....	.....
	4300–14 x 4364– 1	5198	52	.....	.....
	4307– 9 x 4042– 2	5183, 5184	60	.....	.....
	Total, 4 progenies		148	.....	.....
2	2036–9 x 2192–14	4320	.....	9	.....
	4725–2 x 5095–30	A96, A97	.....	67	.....
	Total, 2 progenies		.....	76	.....
3	2025–12 x 2192–14	2335	.....	.....	24
4	2019– 29 x 1946– 4	2398, 2399	30	.....	19
	– 40 x 2192–18	2365, 4340	5	.....	5
	– 63 x –18	2358, 4349	11	.....	10
	– 92 x 1945–10	2385	13	.....	12
	– 98 x –10	2375	11	.....	12
	–104 x 2012– 1	2363	13	.....	12
	–106 x 2192–18	2359, 4351	27	.....	15
	Total, 7 progenies		110	.....	85
5	2019–33 x 2192–18	2352, 4342	.....	5	4
	–51 x 1946– 4	2361, 4347	.....	19	15
	–57 x 2192–18	2369, 2370, 4345	.....	8	14
	–73 x 1945–11	2377, 2378	.....	2	6
	–84 x –10	2382, 4352	.....	22	26
	Total, 5 progenies		.....	56	65
6	2019–17 x 1945–11	2396, 2397	.....	.....	43
	–19 x –11	2381	.....	.....	19
	–25 x –11	2351, 4344	.....	.....	44
	Total, 3 progenies		.....	.....	106

TABLE 17. F_2 AND BACKCROSS PROGENIES OF DILUTE SUN RED IVa x GREEN VIc

Group	Pedigree nos.		Number of F_2 plants	
	F_1	F_2	Dilute sun red IVa	Green VIc
1	1983–34	4502, 4503	27	11
	2854– 7	4677–4679	199	73
	2866– 1	6471, 6472	43	15
	Total, 3 progenies		269	99
	F_1 x VIc			
2	2854–13 x 2887–69	6325, 6326	87	96
	–16 x –69	6319–6321	42	45
	2861– 1 x –41	4686–4688	93	100
	2866– 2 x 2888– 2	5748–5750, 6485–6487	90	74
	4707–82 x 4685– 1	6533–6535	45	43
	Total, 5 progenies		357	358

TABLE 18. F_1 PROGENIES OF INTERCROSSES BETWEEN GREEN PLANTS, VIa, VIb, AND VIc

Group	Pedigree nos.		Number of F_1 plants	
	P_1	F_1	Brown V	Green VI
1	2019–25 x 2019–106	2354	.....	23
2	2019–25 x 2019–33	2350, 4343	.....	22
3	2019– 40 x 2019– 63	2367	.....	25
	– 98 x – 40	2376	.....	25
	–104 x –106	2362	.....	22
	Total, 3 progenies		.....	72
4	2019–57 x 2019–51	2371, 4346	.....	24
5	2019– 33 x 2019–63	2355	6	19
	– 40 x –33	2366, 4341	8	28
	– 57 x –98	2372, 4350	14	26
	– 73 x –40	2380	7	16
	–106 x –51	2360	5	16
	Total, 5 progenies		40	105

TABLE 19. F_2 PROGENIES OF CROSSES BETWEEN BROWN V AND GREEN VIc

Pedigree nos.		Number of F_2 plants	
F_1	F_2	Brown V	Green VIa, b, c
1514–12	2029	19	16
–23	2031	22	13
–38	2028	25	16
2983– 7	5071, 5072	40	44
–11	5070	15	11
2986– 4	5078	21	8
– 9	5077	46	36
4035–35	5110	14	6
4068– 4	5225	53	23
–10	5227	24	20
–11	5226	38	30
Total, 11 progenies		317	223

TABLE 20. F_3 PROGENIES FROM F_2 BROWN PLANTS OF THE CROSS BROWN V x GREEN VIc

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Brown V	Green VI
1	2031–28	4323	19	.....
	–32	2323	10	.....
	Total, 2 progenies		29	.....
2	2031–20	2324, 2541, 2542, 2948, 2949	82	34
	–29	2327, 2328	18	6
	Total, 2 progenies		100	40
3	2029–27	2320, 4321	17	20
	–34	2315, 4322	22	19
	Total, 2 progenies		39	39

TABLE 21. F_2 PROGENIES OF THE CROSSES SUN RED IIa x GREEN VIc AND DILUTE SUN RED IVa x GREEN VIa

Group	Pedigree nos.		Number of F_2 plants		
	F_1	F_2	Sun red IIa	Dilute sun red IVa	Green VIa, c
1	1514–32	2040, 4294	53	16	19
	–76	2041, 4295	40	14	23
	2083– 1	4336, 4337	24	10	11
	– 2	4338, 4339	26	4	11
	2981– 3	4992, 4993	91	42	45
	– 4	4994–4996	203	55	84
	4014– 1	5554–5557	83	33	33
	– 3	5559–5563	47	13	13
	4019– 2	5691, 5692	28	6	18
	– 4	5685, 5686	20	2	12
	4020– 1	5708	28	12	10
	4035– 3	5111–5113	49	21	24
	4040– 2	5148, 5149	14	5	13
	6661– 9	7379	35	16	21
	6662– 1	7381	44	9	29
	– 8	7380	42	10	17
	Total, 16 progenies		827	268	383
2	2398– 2	4426, 4427	28	9	12
	4029– 1	5097	31	18	21
	4776– 1	6951–6953	127	38	71
	4780– 9	6960, 6961	92	25	42
	–11	6954–6956	65	30	33
	Total, 5 progenies		343	120	179
3	1416– 1 x 1430– 1	1494, 2074	39	39	92
	2888–22 x 4019– 2	5694B, 5695A	16	14	22
	2922–18 x 4014– 3	5563–5565	30	26	68
	4014– 1 x 2922– 1	5558	3	3	10
	4019– 2 x 2888– 1	5697, 5698	15	14	22
	– 4 x – 1	5689, 5690	24	13	31
	4020– 1 x 2887–69	5709	7	14	22
	Total, 7 progenies		134	123	267
4	2921–15 x 4029– 1	5654–5656	28	37	80
	4774– 1 x 4710–45	6945, 6946	78	71	151
	4781– 2 x 4707–35	6967, 6968	54	76	132
	4782– 5 x –18	6972, 6973	103	88	195
	–13 x –15	6974–6978, 7667, 7668	80	101	191
	4789– 4 x –19	6989, 6990	50	43	108
	6661– 9 x 6690–17	7328, 7329	17	17	38
	6790– 5 x 6809–18	7293	32	32	67
	Total, 8 progenies		442	465	962

TABLE 22. F_2 PROGENIES OF THE CROSSES DILUTE PURPLE IIIa x GREEN VIc AND DILUTE SUN RED IVa x GREEN VIb

Group	Pedigree nos.		Number of F_2 plants		
	F_1	F_2	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c
1	1514–61	2044, 2560, 2561	44	14	16
	2019–10	2425, 2931, 2932	19	3	6
	2072– 1	4333, 4334	38	12	10
	– 9	4335	22	13	7
	2956– 2	4899–4904	153	58	73
	4035–33	5107	50	16	24
	4068– 6	5222	46	18	26
	–17	5223	44	15	11
	Total, 8 progenies		416	149	173
2	2361– 1	4424, 4425	14	4	4
	4070– 6	5235, 5236	133	51	52
	–11	5237, 5238	62	21	19
	5269– 3	6696, 6697	30	11	15
	A96–14	A416, A417	15	6	4
	A97–29	A407, A408	30	9	13
	Total, 6 progenies		274	102	107
	6790–1 x 6809–8	7292	26	20	56

TABLE 23. F_2 PROGENIES OF THE CROSS SUN RED IIa x BROWN V

Pedigree nos.		Number of F_2 plants			
F_1	F_2	Purple Ia	Sun red IIa	Brown V	Green VIa
5192–1	A99	14	4	5	1
–2	7767	37	5	9	2
–3	7766, S23	69	20	23	7
Total, 3 progenies		120	29	37	10

TABLE 24. F_2 PROGENIES OF THE CROSS SUN RED IIa x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_2 plants	
	F_1	F_2	Sun red IIa	Dilute sun red IVa
1	413– 1	1298	40	13
	617–11	1235	15	4
	1520– 9	2017	31	8
	2065– 1	4330	14	5
	– 2	2431, 4331	48	15
	2414– 2	2987–2992	36	9
	2975– 4	4983–4986, 7001, 7002	373	123
	4028– 3	5643–5646	22	7
	4040– 3	5150, 5151	41	8
	4332–26	5491–5493	55	16
	4787– 4	6779–6782	166	50
	5165– 2	A114	55	20
	7224– 4	8118, 8119	43	12
	7359– 1	8170, 8171	9	3
	7854– 1	8094, 8095	35	15
	A119– 4	A227	15	6
	Total, 16 progenies		998	314
2	F_1 x IVa			
	2065– 1 x 2043– 2	4329	27	30
	– 2 x – 2	2432, 4332	6	13
	4714–11 x 4774– 1	6943, 6944, 7676, 7677	173	133
	7224– 9 x 7225– 7	8115, 8116	196	180
	7354– 1 x 7315– 5	8250, 8251	86	96
	7770– 1 x 7768–172	8731	16	14
	– 5 x –172	8732	17	11
	A140–14 x A105– 6	A252, A468	92	87
	L1773–15 x L2049– 11	8741	46	37
	–20 x – 10	8742	41	39
	L1844–14 x L2048– 24	8743	37	41
	L2063– 5 x – 8	8746	56	48
	–26 x L2049– 3	8745	7	7
	L2064– 2 x L2048– 22	8744	11	6
	Total, 14 progenies		811	742

TABLE 25. F_3 PROGENIES OF F_2 SUN RED AND DILUTE SUN RED PLANTS OF THE CROSS SUN RED IIa x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Sun red IIa	Dilute sun red IVa
1	2990– 1	5776–5778	.....	10
	4133–26	5366	.....	40
	Total, 2 progenies		.....	50
2	2991–1	5779, 5780	10	.....
	–4	5781	9	.....
	Total, 2 progenies		19	.....
	7001–7 x 7002–11	7684, 7685	101	.....
3	1235– 1	1633–1635, 2009	23	10
	1298–14	2011	14	2
	2987– 2	4997, 4998, 6999, 7000	324	111
	– 9	4999	12	4
	Total, 4 progenies		373	127

TABLE 26. F_2 PROGENIES OF THE CROSS DILUTE PURPLE IIIa x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_2 plants	
	F_1	F_2	Dilute purple IIIa	Dilute sun red IVa
1	483– 3	884	16	5
	848– 2	1574	20	10
	2425– 2	2946, 2947	47	16
	4040– 1	5145–5147	69	26
	4070– 8	5240–5242	65	18
	–15	5234	27	8
	A119– 3	A226	17	4
	Total, 7 progenies		261	87
2	F_1 x IV			
	7317– 6 x 7322– 4	8204, 8205	18	22
	A106– 6 x A140–31	A249, A467	85	95
	A140–12 x A105– 3	A250, A251, A465, A466	83	51
	L1760– 6 x L2026–15	8739	56	63
	L1838–16 x –15	8738	33	32
	Total, 5 progenies		275	263

TABLE 27. F_1 PROGENIES OF THE CROSS SUN RED IIa x DILUTE PURPLE IIIa

Group	Pedigree nos.		Number of F_1 plants		
	P_1	F_1	Purple Ia	Sun red IIa	Dilute purple IIIa
1	1529–18 x 1542–8	2057	10	.....	.....
	6889– 1 x 6835–1	7627	14	.....	.....
	Total, 2 progenies		24	.....	.....
2	2903–2 x 2947–37	4796–4799	74	75	.....
3	488– 9 x 730– 3	842, 1389	18	.....	23
	1529–15 x 1549–35	2058	10	.....	6
	Total, 2 progenies		28	.....	29

TABLE 28. F_2 PROGENIES OF THE CROSS SUN RED IIa x DILUTE PURPLE IIIa

Pedigree nos.		Number of F_2 plants			
F_1 x IVa	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
6650– 9 x 6691– 8	7337	8	12	13	6
6651–10 x – 8	7338	7	7	5	6
7700– 4 x 7768–172	8723, 8724	9	8	6	5
–14 x –172	8725, 8726	13	10	12	15
7769– 2 x –172	8729, 8730	8	14	14	12
– 5 x 7315– 10	8263, 8264	19	22	18	15
– 7 x – 9	8261, 8262	35	37	36	24
Total, 7 progenies		99	110	104	83

TABLE 29. F_2 PROGENIES OF THE CROSS PURPLE Ia x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_2 plants			
	F_1	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
	478– 3	880	53	18	12	4
	– 4	881	49	20	11	5
	479– 1	883	43	15	12	3
	484–24	907, 1531	39	11	13	5
	–26	828, 1396, 1530	74	25	23	10
	739– 1	1312, 1549	97	27	28	8
	849– 1	1553, 1554	40	10	14	2
	850– 3	1559	10	5	0	1
	851– 2	1563	23	5	3	0
	– 3	1565	16	4	7	1
	852– 1	1566, 1567	14	5	3	1
	– 2	1568	2	0	1	1
	1564–15	4102	13	2	1	0
1	2971– 3	4968–4976	65	22	23	8
	4028– 1	5647	17	5	5	0
	– 6	5082, A66	138	41	45	14
	4045– 3	5154	40	10	13	5
	4046– 4	5159, 5160	65	23	18	6
	4070– 4	5239	34	10	9	3
	–12	5232, 5233	7	1	2	2
	5165– 8	A117	40	14	13	5
	5172– 3	A126	17	7	6	1
	5179– 1	A130	42	15	11	7
	– 6	A131	12	1	4	3
	5180– 5	A133	36	11	10	3
	S12–18	A208	27	9	9	2
	Total, 26 progenies		1,013	316	296	100
	F_1 x IVa					
	740– 2 x 732– 1	1118, 1119	39	33	36	35
	1105– 9 x 849– 3	1557, 1558	15	14	14	15
	–15 x – 1	1561, 1562	11	11	7	8
	–16 x 852– 2	1570, 1571	13	10	12	11
	1106–12 x 848– 1	1572, 1573	9	6	12	9
	1107– 4 x 851– 2	1564	4	6	8	4
	–13 x 850– 3	1560	10	7	12	8
	2922–19 x 4046– 4	5161, 5162, A142, A143	37	34	39	30
2	4045– 3 x 2922–18	5155, 5156	23	17	13	17
	4046– 4 x 4042– 2	5164, 5165, A105–A107	26	23	27	26
	4729– 8 x 5165– 8	S12	7	2	5	5
	5812– 3 x 5179– 6	A132	6	9	3	5
	6785– 1 x 6784–18	7429, 7430	10	14	17	9
	– 1 x –26	7431, 7432	31	31	36	26
	7226– 2 x 7268– 2	8111	33	30	32	27
	7263– 9 x 7240–10	8008	14	15	18	14
	A140–18 x A106– 4	A248, A469	35	44	34	40
	Total, 17 progenies		323	306	325	289

TABLE 30. F_3 AND F_4 PROGENIES OF F_2 AND EQUIVALENT F_3 PURPLE PLANTS OF THE CROSS PURPLE Ia x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_3 plants			
	F_2	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	271– 9	496, 497, 722	34	11	9	5
	1312–52	1535, 1577	35	13	9	1
	–59	1536, 2002	42	14	10	2
	4102– 2	5177	25	8	8	3
	5082–23	6742, A68	48	24	18	8
	–33	6743, A69	74	32	22	9
	5159– 3	A147	10	3	2	0
	Total, 7 progenies		268	105	78	28
	1312–59 x 1140–18	1575, 1576, 2000, 2001	26	25	24	21
2	271– 5	489, 490	12	5	.....	.....
	1312–87	1537	34	16	.....	.....
	5160– 8	A149	14	1	.....	.....
	Total, 3 progenies		60	22	.....	.....
	148– 1 x 271– 5	478, 479	12	6	.....	.....
	1312–87 x 1140–18	1578	9	13	.....	.....
	4102–13 x 4042– 2	5179, 5180, A113	11	12	.....	.....
	Total, 3 progenies		32	31	.....	.....
3	271– 3	492, 493	49	.....	10	.....
	1312–50	1534	44	.....	18	.....
	–81	1581	43	.....	11	.....
	4102–12	5178	26	.....	9	.....
	Total, 4 progenies		162	.....	48	.....
	271–12 x 80–8	483, 484	17	.....	15	.....
	F_3	F_4	Number of F_4 plants			
4	722– 5 x 720– 1	739, 762, 856, 1550	41	54	.....	.....
	A68–31	A339	13	5	.....	.....
5	722–3 x 719–3	740, 761, 849, 850	40	.....	44	.....
	–3 x 721–7	848	12	.....	8	.....
	Total, 2 progenies		52	.....	52	.....
6	722–1	760, 905, 1121, 1526	69	.....	.....	.....
	724–1 x 722–1	857	18	.....	.....	.....

TABLE 31. F_3 PROGENIES OF SUN RED, DILUTE PURPLE, AND DILUTE SUN RED F_2 PLANTS OF THE CROSS PURPLE Ia x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_3 plants		
	F_2	F_3	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	1312– 4	1579	17	.....	.....
	–36	1542	18	.....	.....
	–55	1543	18	.....	.....
	Total, 3 progenies		53	.....	.....
	1312–38	1580, 2010	24	.....	7
	5159– 8	A148	14	.....	5
	A132– 3	A233	16	.....	7
	A133–12	A193	16	.....	5
	Total, 4 progenies		70	.....	24
2	80– 4	487, 488	.....	30	.....
	271– 4	494	.....	50	.....
	A117–12	A473	.....	17	.....
	Total, 3 progenies		.....	97	.....
	271– 1	491	.....	55	25
	– 7	495	.....	42	16
	1312– 3	1538	.....	46	16
	–65	1539, 1999	.....	36	12
	5234– 1	A86	.....	11	5
	– 8	A87	.....	27	12
	Total, 6 progenies		.....	217	86
3	80– 8	485, 486	.....	.....	19
	1312–11	1544, 1872	.....	.....	27
	A133– 3	A192	.....	.....	26
	Total, 3 progenies		.....	.....	72

TABLE 32. F_2 PROGENIES OF THE CROSS WEAK SUN RED IIb x DILUTE SUN RED IVa

Pedigree nos.		Number of F_2 plants	
F_1	F_2	Weak sun red IIb	Dilute sun red IVa
2187–21	4135, 5371	151	41
–23	4133, 5365	160	59
2189–16	4138, 5377	112	25
2190– 4	5373	122	44
– 4 x 2187– 1	4142, 5374	99	42
– 7 x –23	4143, 5376	176	75
– 7	2391, 4144, 5375, 7072	141	49
4022– 5	5715	17	7
4134–22	5370	35	14
–56	5378	89	27
4162–41	5411	17	3
5364– 6	A58	181	43
Total, 12 progenies		1,300	429

TABLE 33. F_3 PROGENIES OF THE CROSS WEAK SUN RED IIb x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Weak sun red IIb	Dilute sun red IVa
1	4136–43	5384, 6805, 7740	77	.....
2	4136–11	5383, 6802	86	39
	4138–15	5385	22	8
	5365–26	A61	13	5
	5371–23	6798	7	2
	Total, 4 progenies		128	54
3	4143–23	5392, 5393	.....	95

TABLE 34. F_2 PROGENIES OF THE CROSSES WEAK PURPLE Ib x DILUTE PURPLE IIIa, WEAK PURPLE Ib x DILUTE SUN RED IVa, AND WEAK SUN RED IIb x DILUTE PURPLE IIIa

Group	Pedigree nos.		Number of F_2 plants			
	F_1 x IIIa, IVa	F_2	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa
1	A208–15 x A445– 1..	A822.....	4	.....	4	.....
	A452– 4 x 7302– 4..	A789, A790.....	53	.....	57	.....
	–18 x –44..	A791, A792.....	84	.....	102	.....
	Total, 3 progenies.....		141	.....	163	.....
2	7507– 2 x A438– 5..	A793–A796.....	77	86	61	56
	A292–17 x A441– 6..	A788.....	55	58	49	38
	A441– 2 x 7515– 3..	A783.....	76	80	69	108
	– 6 x – 8..	A784.....	64	68	69	88
	– 7 x – 8..	A785.....	68	60	66	53
	–12 x A339–10..	A786.....	64	70	69	103
	–18 x 7515– 4..	A787.....	77	104	77	91
	Total, 7 progenies.....		481	526	460	537
3	S27–2 x 6805–9.....	7773, 7774.....	21	28	22	27

TABLE 35. F_2 PROGENIES OF THE CROSS GREEN IVg x BROWN V

Pedigree nos.		Number of F_2 plants					
F_1	F_2	Purple Ia, g	Sun red IIa, g	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green IIIg, IVg, VI
2400– 1.....	2958–2961...	19	5	6	1	5	2
2952– 1.....	4844–4860...	59	21	8	1	14	18
–11.....	4861–4871...	43	15	7	4	11	15
–24.....	4872–4884...	42	12	9	2	15	16
–32.....	4885–4898...	62	23	12	3	20	17
2953–10.....	4822–4829...	84	24	25	8	23	30
Total, 6 progenies		309	100	67	19	88	98

TABLE 36. F_2 PROGENIES OF THE CROSS GREEN IVg x BROWN V

Pedigree nos. F_2	Number of F_2 plants									
	Purple			Sun red			Dilute purple	Dilute sun red	Brown	Green
	Purple anthers Ia	Green anthers Ig	? anthers I	Pink anthers IIa	Green anthers IIg	? anthers II	Purple anthers IIIa	Pink anthers IVa	Green anthers V	Green anthers IIIg, IVg, VI
2958–2961	14	5	0	1	1	3	6	1	5	2
4822–4829	61	12	11	10	4	10	25	8	23	30
4844–4860	42	16	1	10	7	4	8	1	14	18
Total, 3 progenies	117	33	12	21	12	17	39	10	42	50

TABLE 37. F_2 PROGENIES OF THE CROSS PURPLE Ig x GREEN VIc

Group	Pedigree nos.		Number of F_2 plants					
	F_1	F_2	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green
			(Ia, g)	(IIa, g)				(IIIg, IVg, VI)
1	5534–39	6795, 6796	65	11	6	7	15	26
	6655– 6	7376	15	2	3	2	5	1
	Total, 2 progenies		80	13	9	9	20	27
	F_1 x VIc		(Ia)	(IIa)				(VI)
2	6655– 6 x 6690–17	7349	6	13	13	15	17	46
	6808–13 x 6790– 8	7290	30	16	18	16	14	49
	Total, 2 progenies		36	29	31	31	31	95
	F_1 x IVa							
3	6779–2 x 6790–8	7299, 7300	27	25	30	31	.....	.....
	6792–2 x –8	7297	29	29	19	32	.....	.....
	–8 x –8	7296	59	43	46	48	.....	.....
	Total, 3 progenies		115	97	95	111	.....	.....
	F_1 x IVg		(Ia, Ig)	(IIa, IIg)				(IIIg, IVg)
4	6656–9 x 6652–6	7344	23	15	10	15	.....	13

TABLE 38. F_2 PROGENIES OF THE CROSSES PURPLE Ig x DILUTE SUN RED IVa AND PURPLE Ia x GREEN IVg

Group	Pedigree nos.		Number of F_2 plants				
	F_1	F_2	Purple Ia, g	Sun red IIa, g	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg
1	2954–3..	5042–5045.	43	14	13	5	7
	2956–3..	4905–4914.	144	42	25	14	7
	–4..	4915–4929.	56	15	21	3	6
	Total, 3 progenies....		243	71	59	22	20
2	2421–1..	2910, 2911.	14	7	5	1	1
	–2..	2908, 2909.	26	13	4	1	0
	Total, 2 progenies....		40	20	9	2	1

TABLE 39. F_3 AND F_4 PROGENIES FROM F_2 AND EQUIVALENT F_3 PURPLES OF THE CROSS PURPLE Ia x GREEN IVg

Group	Pedigree nos.		Number of F_3 and F_4 plants				
	F_2 and F_3	F_3 and F_4	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Green
1	2909–16.....	5251, 5252	(Ia, g) 9	(IIa, g) 4	3	0	0
	F_2 x IVg 2909–4 x 2884–21	5255.....	15	15	5	1	(IIIg, IVg) 9
	F_2 x VIc 2909–4 x 2887–38	5256, A94.	(Ia) 27	(IIa) 19	15	14	.....
2	5251–6.....	6708.....	31	7	.....	.....	.....
3	2909–9.....	5257, 5258	(Ig) 14	(IIg) 2	.....	.....	5
	5252–1.....	6652.....	23	9	.....	.....	9
	Total, 2 progenies.....		37	11	.....	.....	14

TABLE 39 (*concluded*)

Group	Pedigree nos.		Number of F_3 and F_4 plants				
	F_2 and F_3	F_3 and F_4	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Green
3 (*continued*)	F_2, F_3 x IVg		(Ig)	(IIg)			(IIIg, IVg)
	2909– 9 x 2884–21	5259, 5260, 7007, 7008, 7060, 7061.	19	18	.....	.....	34
	4717–71 x 5252– 1	6654A.....	11	8	.....	.....	13
	5252– 1 x 5669– 3	6654B.....	4	6	.....	.....	6
	Total, 3 progenies.....		34	32	.....	.....	53
	F_2, F_3 x VIc		(Ia)	(IIa)			
	2909– 9 x 2887–38	5261, 5262.	14	11	7	11	.....
	4057– 1 x 2909– 9	5534, 6790.	16	10	13	18	.....
	5251– 1 x 5813–18	6655.....	9	16	7	14	.....
	5813–18 x 5251– 1	6656.....	5	11	6	9	.....
	Total, 4 progenies.....		44	48	33	52	.....
4			(Ig)				(IIIg)
	2909–34.....	5253, 5254, 7090.....	26	.....	.....	.....	6
	5251– 7.....	6658, 7015.	30	.....	.....	.....	12
	Total, 2 progenies.....		56	.....	.....	.....	18
	F_3 x IVg						
	4717–20 x 5251–7..	6659, 7014.	28	.....	.....	.....	27

TABLE 40. F_3 AND EQUIVALENT F_4 PROGENIES FROM F_2 AND F_3 SUN REDS AND DILUTE PURPLES OF THE CROSS PURPLE Ia x GREEN IVg

Group	Pedigree nos.		Number of F_3 and F_4 plants		
	F_2 and F_3	F_3 and F_4	Sun red	Dilute purple IIIa	Dilute sun red IVa
			(IIa)		
1	2090–20	5278	30	.....	8
	5251– 8	6648	37	.....	10
	–10	6709	30	.....	8
	Total, 3 progenies		97	.....	23
			(IIa, g)		
2	2909– 8	5270–5273	43	.....	.....
	–26	5280–5283	64	.....	.....
	–32	5274–5277	121	.....	.....
	Total, 3 progenies		228	.....	.....
	F_2 x IVg				
	2909–26 x 2884–35	5284–5287, 7137	41	.....	.....
	F_2 x VIc		(IIa)		
	2909–26 x 2887–38	5288, 5289	67	.....	.....
	Total, 2 progenies		108	.....	.....
3	2909–21	5265, 5266	.....	46	9
	F_2 x IVg				
	2909–21 x 2884–35	5267, 5268	.....	44	31
	F_2 x VIc				
	2887–31 x 2909–21	5269	.....	41	51
	Total, 2 progenies		.....	85	82

TABLE 41. F_2 PROGENIES OF THE CROSS PURPLE Ig x GREEN IVg

Group	Pedigree nos.		Number of F_2 plants				
	F_1	F_2	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg
1	5255 – 6	7094, 7095, 7701, 7702	(Ig) 80	(IIg) 24	.....	.....	55
	5259 – 3	7010, 7011	54	22	.....	.....	25
	6654B– 3	7375	23	7	.....	.....	9
	6659 –15	7365	28	12	.....	.....	12
	–22	7366	11	3	.....	.....	5
	–27	7368, 8491	43	17	.....	.....	24
	6660 – 9	7378	21	7	.....	.....	10
	–12	7377	33	13	.....	.....	10
	Total, 8 progenies		293	105	.....	.....	150
2	F_1 x IVa		(Ia)	(IIa)			
	6659–19 x 6691–8	7339	14	9	14	12	.....
	6660– 3 x –8	7340	9	11	12	11	.....
	F_1 x VIc						
	6654A–2 x 6690– 9	7335	20	15	13	10	.....
	B–1 x –17	7336	15	26	23	37	.....
	Total, 4 progenies		58	61	62	70	.....

TABLE 42. F_2 PROGENIES OF THE CROSS DILUTE PURPLE IIIa x GREEN IVg

Group	Pedigree nos.		Number of F_2 plants		
	F_1	F_2	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg
1	2403–1	2962–2966	23	8	10
2	2420– 1	2904, 2905	17	5	9
	2954– 4	5038–5041	63	26	34
	2967– 2	6826, 6827	36	8	17
	–11	6828, 6829	78	32	31
	5263– 4	6669, 6670	31	16	8
	5267– 5	6675–6678	41	14	27
	–12	6679–6682	62	12	22
	Total, 7 progenies		328	113	148
3	F_1 x IVg				
	7322–3 x 7317–4	8210–8213	46	45	86

TABLE 43. F_3 AND F_4 PROGENIES FROM F_2 AND EQUIVALENT F_3 DILUTE PURPLES, DILUTE SUN REDS, AND GREENS, OF THE CROSS DILUTE PURPLE IIIa x GREEN IVg

Group	Pedigree nos.		Number of F_3 and F_4 plants		
	F_2 and F_3	F_3 and F_4	Dilute purple IIIa	Dilute sun red IVa	Green
					(IIIg, IVg)
1A	2966– 7	5049–5055	50	25	26
	5049–25	6816–6818, 7441	52	13	20
	5050– 6	6822–6824, 7058, 7059	41	10	27
	Total, 3 progenies		143	48	73
1B	6676–12	7383	26	10	16
	6828–12	7658–7660	14	4	7
	Total, 2 progenies		40	14	23
2	5052–7	6825, 7323, 7442	27	9	.....
	6676–8	7382, A266	55	14	.....
	Total, 2 progenies		82	23	.....
3	5049–37	6819–6821	62	.....	(IIIg) 16
					(IVg)
4	2905–22	2547–2550	.....	21	9
	5053– 1	6875, 6911, 6912	.....	42	13
	Total, 2 progenies		.....	63	22
5	5050– 1	6874	.....	17	.....
	5054–10	6745, 6872, 6873	.....	108	.....
	5055– 2	6871, 7315	.....	51	.....
	– 5	7515	.....	21	.....
	Total, 4 progenies		.....	197	.....
					(IIIg, IVg)
6	2905– 5	5243, 5244	.....	.....	5
	–19	5245, 5246	.....	.....	13
	5049–13	6913, 6914	.....	.....	11
	5052– 3	6833	.....	.....	24
	– 5	S5	.....	.....	15
	–12	6832	.....	.....	32
	6829– 9	7655–7657	.....	.....	30
	Total, 7 progenies		.....	.....	130

TABLE 44. F_2 PROGENIES OF THE CROSSES SUN RED IIg x GREEN IVg, SUN RED IIa x GREEN IVg, AND DILUTE SUN RED IVa x GREEN IVg

Group	Pedigree nos.		Number of F_2 plants			
	F_1	F_2	Sun red		Dilute sun red	Green
			Pink anthers IIa	Green anthers IIg	Pink anthers IVa	Green anthers IVg
1	4787–6	6983, 6984	.....	122	.....	52
	5284–3	7003–7006	.....	94	.....	25
	Total, 2 progenies		.....	216	.....	77
2	F_1 x IVg					
	7317–6 x 7318–4	8214–8217	22	31	24	32
	7318–1 x 7317–4	8222–8225	38	25	34	26
	–4 x –6	8218–8221	45	34	47	51
	Total, 3 progenies		105	90	105	109
3	5267–3	6671–6674	.....	.....	55	22
	F_1 x IVg					
	7031–14 x 6857–5	7725, 7726	.....	.....	30	30

TABLE 45. F_1 PROGENIES OF CROSSES OF SUN RED IIa AND DILUTE SUN RED IVa WITH GREEN IIIg AND IVg

Group	Pedigree nos.		Number of F_1 plants			
	P_1	F_1	Purple Ia	Dilute purple IIIa	Dilute sun red IVa	Green
1	IIa x IIIg					
	7097–5 x A159–25	7710	33	.....	.....	.....
	7357–3 x 7356– 1	8151, 8152	31	.....	.....	.....
	Total, 2 progenies		64	.....	.....	.....
	IVa x IIIg					
	A9–22 x 7097–1	7709	.....	4	.....	.....
2	IVa x IVg					
	6860– 8 x 6869–1	7713	.....	.....	28	.....
	A9–14 x 7060–1	7708, A283, A284	.....	.....	31	.....
	Total, 2 progenies		.....	.....	59	.....
	IVa x IIIg					
	6860–13 x 6871–39	7714	.....	11	12	.....
	6861– 2 x 6751– 3	7711	.....	9	18	.....
	Total, 2 progenies		.....	20	30	.....
	IVa x IIIg					(IIIg, IVg)
	6861–4 x 6882–5	7512, 7513, 7716	.....	25	11	34
	7039–3 x 7061–1	7727, 7728	.....	44	43	72
	Total, 2 progenies		.....	69	54	106
3	IVa x IIIg					(IIIg)
	7312–8 x 7313–2	8183	.....	86	.....	92
	7313–2 x 7314–1	8184	.....	31	.....	19
	7314–1 x 7313–1	8200, 8201	.....	126	.....	129
	–6 x –2	8185	.....	85	.....	98
	Total, 4 progenies		.....	328	.....	338

TABLE 46. F_2 PROGENIES OF THE CROSS GREEN IVg x GREEN VIc

Group	Pedigree nos.		Number of F_2 plants	
	F_1	F_2	Dilute sun red IVa	Green
				(IVg, VIc)
1	5534–4	6791, 6792	35	29
	6530–1	7179, 7180	51	43
	–2	7181, 7182	32	30
	6531–1	7177, 7178	64	42
	–2	7175, 7176	63	38
	7032–1	7163, 7164	52	39
	7036–3	7169, 7170	60	36
	7037–2	7171, 7172	63	34
	Total, 8 progenies		420	291
	F_1 x VIc			(VIc)
2	7032–7 x 6878–42	7729, 7730	24	24
	7034–5 x –42	7767, 7768	42	34
	Total, 2 progenies		66	58
	F_1 x IVg			(IVg)
	7037–4 x 7049–7	7173, 7174	48	50
	7049–1 x 7037–4	7731, 7732	48	46
	Total, 2 progenies		96	96

TABLE 47. F_3 PROGENIES OF F_2 DILUTE SUN RED PLANTS OF THE CROSS GREEN IVg x GREEN VIc

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Dilute sun red IVa	Green IVg, VIc
1	6791– 3	7148, 7149	23	19
	6792– 6	7154, 7155	69	45
	–11	7159	16	13
	Total, 3 progenies		108	77
2	6791–22	7150, 7151	65	23
	–23	7152, 7153	49	18
	6792– 7	7157	38	12
	–10	7158	23	10
	–13	7160	12	3
	Total, 5 progenies		187	66
3	6792– 5	7156	48	.....
	–25	7161	30	.....
	Total, 2 progenies		78	.....

TABLE 48. F_2 AND F_3 PROGENIES OF THE CROSS GREEN IVg x GREEN VIa

Group	Pedigree nos.		Number of F_2 and F_3 plants		
	F_1	F_2	Sun red	Dilute sun red IVa	Green
			(IIa, g)		(IVg,VIa,c)
1	2400– 2	2902, 2903	7	3	5
	2952– 5	4838–4843	36	3	18
	–22	4830–4837	99	15	57
	2953– 4	4810–4813	88	32	59
	– 7	4814–4817	111	20	62
	–21	4818–4821	92	30	45
	2957– 2	4930, 4931	153	58	102
	Total, 7 progenies		586	161	348
	F_2	F_3			
2	4930–31	6991, 6992	119	.....	.....
			(IIa)		(VIa)
3	2903– 2	4783–4786	99	.....	32
	4930–22	6993, 6994	130	.....	39
	Total, 2 progenies		229	.....	71
	F_2 x IVa				
	2903–2 x 2889–38	4787–4790	55	.....	.....

TABLE 49. F_2 PROGENIES OF THE CROSS GREEN IIIg x GREEN VIc, AND F_1 PROGENIES OF CROSSES OF F_2 GREENS WITH SUN RED IIa AND DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_2 plants				
	F_1	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg, VIb, c
1	2907–8	5297, 5298	.....	.....	28	11	38
	5262–5	7085, 7086, 7722, 7723	.....	.....	81	26	97
	Total, 2 progenies		.....	.....	109	37	135
	P_1	F_1	Number of F_1 plants				
2	IIIg x IIa 7085–10 x A159–24	7717	27	.....	.....	.....	.....
	IIIg x IVa 7086–2 x 7102–7	7207	.....	.....	14	.....	.....
	–3 x –8	7719	.....	.....	25	.....	.....
	Total, 2 progenies		.....	.....	39	.....	.....
3	IIIg x IIa 7086–6 x A159–17	7718, A298, A299	28	41	.....	.....	.....
	IIIg x IVa 7086–4 x 7102–8	7720	.....	.....	11	9	.....
4	IVg x IVa 7086–8 x 7102–8	7721	.....	.....	.....	22	.....

ANTHER, GLUME, AND RACHIS COLOR OF PURPLE

1, Purple, type Ia, typical, anthers purple; 2, type Ia with r^{ch}, anthers near-black; 3, type Ia with pr, anthers reddish; 4, type Ig, with R^g or r^g, anthers green (Drawings by C. W. Redwood, somewhat diagrammatic)

ANTHER, GLUME, AND RACHIS COLOR OF DILUTE PURPLE AND GREEN

1, Dilute purple, type IIIa, typical, anthers purple; 2, type IIIa with r^{ch}, anthers near-black; 3, type IIIa with *pr*, anthers reddish
4, Green, types IIIg and IVg with R^g or r^g, green thruout

(Drawings by C. W. Redwood, somewhat diagrammatic)

ANTHER, GLUME, AND RACHIS COLOR OF SUN RED AND DILUTE SUN RED

1, Sun red, type IIa, intensely pigmented form
2, Dilute sun red, type IVa, intensely pigmented form; 3 and 4, near-green forms, little color in glumes, anthers green with reddish stippling as shown in enlarged anther

(Drawings by C. W. Redwood, somewhat diagrammatic)

ANTHER, GLUME, AND RACHIS COLOR OF BROWN AND GREEN

1, Brown, type V, intensely pigmented, homozygous form; 2, type V, less intensely pigmented form, heterozygous for *B* or *Pl* or both
3, Green, type VIc; 4, type VIb, green with tinge of brown due to *Pl* and *rch*
(Drawings by C. W. Redwood, somewhat diagrammatic)

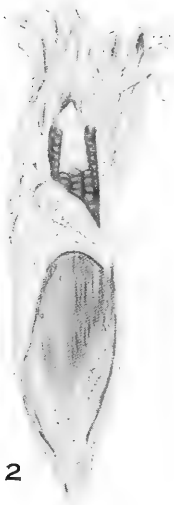
CULM, HUSK, AND SHEATH COLOR OF PURPLE AND SUN RED

1, Purple, type Ia; 2, weak purple, type Ib
3, Sun red, type IIa; 4, weak sun red, type IIb; 5, type IIb, inner husks of lower ear highly colored from exposure to sunlight directly after being torn apart
(Drawings 1 and 3 by C. W. Redwood; 2, 4, and 5 by Bernice M. Branson)

CULM, HUSK, AND SHEATH COLOR OF DILUTE PURPLE, DILUTE SUN RED, BROWN, AND GREEN

1, Dilute purple and dilute sun red, types IIIa and IVa; 2, more highly colored form of types IIIa and IVa
3, Brown, type V
4, Green, types VIb and VIc; 5, type VIa, with some brown in outer husks due to *B*

(Drawings by C. W. Redwood)



MATURE CULM, HUSK, AND COB COLOR

1, Purple, type Ia; 2, sun red, type IIa; 3, dilute purple, type IIIa; 4, more intensely pigmented form of type IIIa; 5, brown, type V; 6, dilute sun red, type IVa

(Drawings by Carrie M. Preston)

DEVELOPMENT OF COLOR IN DARKNESS

Tassels and sheaths developed under black paper bags: 1, purple, type Ia; 2, brown, type V; 3, dilute purple, type IIIa; 4, sun red, type IIa, no red color

(Drawings by Carrie M. Preston)

RELATION OF SOIL FERTILITY TO COLOR DEVELOPMENT

Young plants of dilute sun red, type IVa: 1, plant grown in fertile soil; 2, plant grown in infertile soil

(Drawing 1 by Bernice M. Branson; 2 by Carrie M. Preston)

COLOR DEVELOPMENT IN BROKEN LEAVES

1, Dilute sun red, type IVa, about one week after the leaf was creased; 2, dilute purple, type IIIa with japonica white stripes, about three days after the leaf was creased

(Drawings by Carrie M. Preston)

ABERRANT COLORATION OF BROWN TASSEL

Poorly developed tassels of brown, type V, sometimes exhibit purple in abnormally developed parts

(Drawing by Carrie M. Preston)

JLY, 1921 MEMOIR 40

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

IBERATION OF ORGANIC MATTER BY ROOTS OF GROWING PLANTS

T. L. LYON AND J. K. WILSON

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LIBERATION OF ORGANIC MATTER BY ROOTS OF GROWING PLANTS

LIBERATION OF ORGANIC MATTER BY ROOTS OF GROWING PLANTS

T. L. Lyon and J. K. Wilson

In the course of an investigation under way at this station, it became desirable to know whether organic matter, particularly that of a nitrogenous nature, is liberated by the roots of growing plants, at least of the plants commonly raised on farms in this region. Numerous investigations conducted elsewhere have shown that nitrogen is lost by certain plants during the late stages of growth, particularly about the ripening period. There seemed to be a question, however, whether this nitrogen escaped from the leaves or the roots, and it had never been shown to be in the form of organic matter. The previous investigations had, indeed, not touched on the question of the loss of organic matter by growing plants, and aside from its bearing on the investigation in hand this appeared to be a matter of some scientific interest.

A closely related question is the possible liberation of reducing or oxidizing substances by the roots of growing plants. There had previously been some investigation of this subject, but since the experiments on the liberation of organic matter furnished exceptionally good opportunities for making the tests for catalysts it was decided to try to obtain some information to supplement the previous work.

REVIEW OF LITERATURE CONCERNING LOSS OF NITROGEN FROM GROWING PLANTS

A large amount of work has been reported showing the percentage of the various nutritive elements found in crops at certain stages of growth. Less work has been done, however, on the actual weight of nutrients in plants during their growth and maturity.

The work of Wilfarth, Römer, and Wimmer (1906) was concerned with the assimilation of the elements of nutrition by plants during different periods of their growth. This investigation extended over a period of about eight years. The experiments included both field and pot work, the former with barley, spring wheat, and potatoes, and the latter with

barley, peas, potatoes, and mustard. The plants were harvested at different stages of growth. These plants were carefully divided into their component parts — roots, stems, ears, and so on — and were dried, weighed, and analyzed. The results as stated below are based on pounds of nitrogen in the crop.

The barley was planted on March 30 and the cuttings were made on May 29, June 17, July 3, and July 27. The plant parts were separated and grouped into aboveground parts and underground parts. Separate analyses were made of stems, green leaves, yellow leaves, ear stalks, awns, straw, grain, roots, and stubble. Total weights of nitrogen showed that this nutrient was present in its greatest amount on June 17 (presumably when the plants were in bloom) and that the mature cutting of July 27 had lost 25 per cent of the total nitrogen.

The wheat was planted on April 23 and was harvested on June 22, July 14, August 5, and August 28. The methods used were the same as for barley. In the case of the wheat, the nitrogen was found in its greatest amount in the third cutting, on August 5, and the mature crop showed a loss of about 20 per cent of the total nitrogen.

The potatoes were planted on April 28 and analyses were made of the various parts of the plant. Four different harvests were gathered as the crop was maturing. The results were quite different from those with barley or with wheat. In this case the greatest amount of nitrogen was found in the last harvest, which represents the crop gathered in October.

The barley was planted on April 20 in sand in pots, and was watered with nutrient solutions. Quadruplicate cultures were grown in the greenhouse. On May 11 stems had commenced to show. The first harvest was made on May 24, the second on June 1, the third on June 12, the fourth on June 25, the fifth on July 20. The harvest consisted of both roots and tops. In one series the greatest weight of nitrogen was found on June 25, in the other three on June 12. From these dates on to maturity there was a loss of total nitrogen ranging from 9 to 26 per cent.

The peas were planted and tended in a similar manner to the barley, with the same dates for planting and harvesting. The weight of nitrogen in the harvested crops was greatest on June 25 in three cases, and in the fourth case at the last harvest. The decrease toward maturity in the three cases ranged from 9 to 30 per cent.

The potatoes were grown in turf and sand in the greenhouse. Applications of fertilizer were made so that plant nutrients would not be deficient. Harvests were made on June 12, June 30, August 7, and September 14. The plant parts were divided into foliage and tubers. The figures for weight of nitrogen show that there was a constant decrease of this constituent in the foliage after the first harvest, altho there was a constant increase in the weight of the tubers. The total plant, however, had its greatest amount of nitrogen on August 7, with a decrease of 6.46 per cent thirty-eight days later.

Pots containing 5.3 kilograms of dry earth received fertilizers to stimulate growth of plants and to furnish an abundant supply of nutrients. The seeding of mustard was done on May 7, and subsequently all pots contained six plants. The experiment was run in duplicate. The mustard was harvested, first, on the appearance of the first pods, second, when the formation of seed was complete, and third, at maturity. Analysis of the total plant only was made. The total nitrogen was greatest when the formation of seed was complete. The loss at the third harvest was about 10 per cent of the total nitrogen.

With the intention of verifying the results obtained by Wilfarth, Römer, and Wimmer, André (1912) cut barley at five different stages of growth from equal areas of land and analyzed the dry harvest. The cuttings were made (1) when the heads began to show, (2) when the barley was in bloom, (3) when seed began to form, (4) at the mature stage, and (5) beyond the ripe stage. The figures for total nitrogen show 7.023 grams at the first stage, 8.693 at blooming, 10.422 when the fruit was forming, 12.389 at maturity, and 10.360 at the last harvest.

The object of an experiment by Ramsay and Robertson (1918) was to determine the relative proportions of each of the principal nutrient elements contained in the plant at various stages of growth. They grew potatoes in soil in boxes containing about 130 pounds of well-drained and fertilized soil. Approximately the same weight of seed was put in each box. The first harvest was gathered on January 29, thirty-three days after brairding, the second on February 25, the third on March 26, and the last on April 30. At the first three harvests complete recovery of tops and roots was made. The last harvest was more difficult and about 30 per cent of the roots were lost. Cropping, harvesting, and analyzing were done in duplicate in each case. The total nitrogen contained in a 20-ton crop of

potato plants at various stages of development was 69 pounds at the first harvest (thirty-three days), 241.3 pounds at the second harvest (fifty-eight days), 306.7 pounds at the third harvest (eighty-nine days), and 319 pounds at the fourth harvest (one hundred and twenty-four days). There was a constant assimilation of this important element.

Hay was cut by Crowther and Ruston (1911–12) from uniform areas of a crop of grass which had been seeded the previous spring. The grass seed consisted of a mixture of perennial rye grass, Italian rye grass, white clover, trefoil, alsike, English single-cut cow grass, Chilean red clover, and rib grass. The first cutting was made when the rye grass was in full flower. A good growth of leguminous plants showed underneath. The second cutting was made when the rye grass was forming seed and the clovers were beginning to flower. At the third cutting the grasses were ripening and the clovers were in full bloom, while the fourth and last cutting was made when the crop was decidedly ripe. Analysis of the crops showed the greatest total weight of nitrogen to be present at the third cutting, or when the grasses were ripening and the clovers were in full bloom. In the last cutting there was a loss of 25 pounds of nitrogen to the acre.

The work was repeated the following year, but with barley as the crop. The seed was drilled on May 12. Cuttings were made on June 9, June 23, July 7, and July 21, but the stages of growth reached on these dates were not noted. The changes with advancing age as to nitrogen were similar to those observed in the preceding year with grasses.

The changes in chemical composition of the timothy plant during growth and ripening, with comparative studies of the wheat plant, are recorded by Trowbridge, Haigh, and Moulton (1915). Timothy plants, cut from uniform areas, represented the following stages of growth: (1) about one foot high in rapid growth; (2) no heads showing; (3) no stalks in bloom but beginning to head; (4) in full bloom; (5) just out of bloom and seed formed; (6) seed in dough; (7) seed fully ripe; (8) growth the following spring not yet started but leaves green. The plant parts of the samples thus collected were divided into heads, stalks and leaves, hay, and stubble and bulbs. The amounts of the various nutrients determined were recorded in total pounds to the acre. Data from these plants were collected for one year only. The figures for weight of nitrogen showed that there was a gradual increase in this constituent in heads from

all plots. In the stalks and leaves, the nitrogen was found in greatest amounts in two cases when the plants were just out of bloom and the seed was formed, and in the third case when no stalks were in bloom but the plants were beginning to head. In the hay the greatest weight of nitrogen was found when the seed was all in dough. In the stubble and bulbs the greatest amount of nitrogen was present when the seed was fully ripe.

The comparative studies with wheat represent two areas from the same field. The stages of development were: (1) plants green and in bloom; (2) seed formed and in milk; (3) seed in dough; (4) seed fully ripe. The plant parts of the samples were divided into heads, stalks and leaves, plants above ground, and roots and stubble. The figures for nitrogen found in the heads showed a steady increase in this nutrient thruout all the stages. With stalks and leaves there was a constant loss of nitrogen after the first stage as the plant approached maturity. In the plants above ground there was an increase of nitrogen to the seed-in-dough stage and a considerable loss in the fully-ripe stage. Roots and stubble contained their greatest weight of nitrogen at the seed-in-milk stage. If the total plant is considered, the nitrogen reached its greatest amount when the seed was in the dough stage.

The influence of advancing maturity on the composition of timothy was reported by Waters (1915). Results were obtained for five years of investigation, but the results are complete for only three of these years. Uniform areas were harvested at five different stages of growth: (1) when the plants were in full head; (2) when the plants were in bloom; (3) when the seed had formed; (4) when the seed was in dough; (5) when the seed was ripe but not shattered. The greatest weight of nitrogen was found in three of the trials when the plants were in full bloom, and in the other two trials when the seed had formed. The fluctuation in loss of nitrogen between the stages when it was at the maximum and when it was fully ripe ranged from 12 to 38 per cent.

Schulze (1904) cut 100 plants of rye and collected the roots for examination. The cuttings were made forty days after drilling, which was on September 20. On April 22 a second cutting was made. The plants at this stage were very green. On May 20 a third cutting was made. The plants now were in the boot stage. The fourth cutting was made on June 16 and the plants were just thru blooming. The weight of nitrogen

in these stages was as follows: first cutting, 0.153 gram; second cutting, 1.225 grams; third cutting, 2.723 grams; fourth cutting, 2.713 grams.

With wheat only three harvests were made: the first was thirty-seven days after drilling, which took place on September 23; the second was on April 22, and no heads were showing at this date; the third was on June 16, when the plants were thru blooming. The nitrogen in 100 plants was as follows: first period, 0.132 gram; second period, 0.596 gram; third period, 1.802 grams. No later analyses are given, and thus it is not clear whether there was a loss in weight of nitrogen after the blooming period.

Le Clerc and Breazeale (1909) state that the loss of nutrients from plants may be explained in one of three ways: (1) by the backward flow of the salts of the plant juices thru the stems and roots to the soil; (2) by the decay or dying and falling off of leaves; or (3) by the action of rain, dew, wind, and other climatic agencies. Or there may be a combination of all these causes to a limited extent. In support of the third possibility, these investigators conducted experiments designed to imitate these climatic agencies. Barley plants were grown in soil contained in Wagner pots, and no water was allowed to come in touch with the aboveground parts during the growing period. Just at the heading period the whole plant was harvested, placed in a large evaporating dish, and soaked with water for several minutes. After drying, this operation was repeated. The plants were then dried and analyzed. The results show that 1.6 per cent of the entire content of nitrogen was lost on washing.

Wheat plants were harvested at three periods of growth — bloom, early ripeness, and full ripeness. The plant parts were divided into stems and straw, and heads. They were separately washed or soaked for from five to ten minutes. The wash water was analyzed, as were also the dried stems and straw and the heads. The results show that at bloom 1.4 per cent of the nitrogen was washed out, while at full maturity 7 per cent was found in the wash water.

Results were obtained also from apple twigs. Two twigs containing green leaves were gathered and washed for a few minutes with distilled water. They were then set aside, with their butt ends immersed in water, until the leaves were unquestionably dead, when they were again washed and analyses were made of both washings and residues. The results of the analyses showed that thru the action of water about 3 per cent of nitrogen had been washed out.

Two pots of wheat were kept in the greenhouse until the wheat was completely ripe. They were then placed out of doors, where they were subjected to four rainfalls on separate days. The pots were so arranged that the washings were caught in a tray. These washings, equivalent to about one inch of rainfall, dissolved from the plant 27 per cent of the nitrogen as well as other nutrients.

Two oat pots were placed out of doors as were the wheat pots. The plants were about eight inches high. They were allowed to grow in this position until they were ripe. They were exposed to three rains during this time. The leachings contained 2 per cent of the nitrogen, as well as other nutrients.

In two pots of potatoes, the aboveground parts were washed with 2.5 quarts of water in a very fine spray. This was done when the plants were twenty-four inches high, when they were beginning to ripen, and when they were completely ripe. The leachings and the plant parts above ground were analyzed. The results show that, due to the action of washing, 7.5 per cent of the nitrogen was washed out.

Jones and Huston (1914) report the composition of the maize crop at stages corresponding in the main with those at which the crop would be used for practical purposes, such as soiling, ensiling, and grain production. Conditions of uniformity were maintained as nearly ideal as it was possible to have them. In order to insure adequate moisture, the field was irrigated when necessary so as to provide not less than one inch of water every week. The soil was in a good state of fertility. Analyses were made as follows: (1) when the plants had six leaves, June 16; (2) when the plants were about four feet high, July 24; (3) when tassels began to form, August 6; (4) when the maize was fully pollinized, August 28; (5) when the plants were in the medium milk stage, with the pollen all shed and the silks brown, September 10; (6) when the kernels were glazing, September 24; (7) when the kernels were hardening, this being the ensiling stage, October 1; (8) when the maize was ready to put into shock, October 8; (9) when the maize was fully cured and ready to be stored, November 12.

The samples represented the crop cut at the soil level. Data for weight of nitrogen showed a gradual increase from the first analysis to October 8, the amount at first being 0.28 pounds an acre and increasing to 110.6 pounds on the last-named date. At the last analysis, on November 12,

which represented samples left in the field and in the shock, for the former a loss of about 23 pounds was shown, while for the latter a slight gain was reported. This loss of nitrogen when the plants were left in the field after October 8 was from both ears and stalks. In the former there was a loss of 9.2 pounds in the field and a gain of 7.6 pounds in the shock; in the latter there was a loss of 15 pounds in the field and a loss of only 2.1 pounds in the shock.

Taking the results of these investigations as a whole, there appears to be in nearly all cases a loss of nitrogen from grass and small grains at some time between the period of full bloom and complete maturity. In maize this occurs if the plants are allowed to ripen when connected with the roots, but potatoes showed no loss of nitrogen in the Bernburg and Australia experiments, and only a small loss in those of Le Clerc and Breazeale.

OBJECT OF THE PRESENT EXPERIMENTS

The experiments herein described had two more or less distinct objects. The first was to ascertain whether growing plants liberate organic matter, and, if they do, to determine at what stage of growth this takes place and what relation it bears to the absorption of nitrate nitrogen by the plant. The second object was to detect, if possible, the presence of reducing and oxidizing ferments in the nutrient solutions in which the plants used for the first investigation were grown.

METHODS USED

The plants used in these experiments were grown in water culture. This was done in order that an intimate study might be made of the plant as it grew and the solution as it was being drawn upon by the plant for various nutrients, especially nitrogen. Since a number of organic bodies may be given off by the developing plant, these may not be present when the nutrient solution is analyzed if it is allowed to become infected with molds or bacteria. Therefore, in order that this solution should represent the action of the plant alone, a method for growing the root system in contact with the nutrient solution without infection was used. This method has been published, together with data showing its reliability (Wilson, 1920). A description of the method follows.

SEED STERILIZATION

Seeds were rendered sterile by the calcium hypochlorite method as employed by Wilson (1915). After disinfection the seeds were planted on a sterile medium, from which, after germination, the plants were transferred to the permanent position. The solid medium for the germination was usually composed of the same ingredients as were used in the large containers, from which the plants eventually drew their nutrients, with from 1 to 1.5 per cent of agar. The agar was used in order that contaminations might be detected before the plants were transferred to their permanent position. This medium was made in sufficient quantity to meet the requirements and was distributed into large test tubes.

Since the roots of most plantlets spread out in a lateral direction, thus making it difficult to transplant them quickly and conveniently, some device was needed which would direct the root growth in a vertical direction. To accomplish this there was placed in each test tube a short piece of glass tubing, 25 by 50 millimeters in size (fig. 1, *e*). A sufficient quantity of the medium was put into the tube to cover all but about 15 millimeters of this glass tubing. After sterilization of the medium the sterile seeds were dropped onto it, where they germinated and produced rootlets for subsequent use. When the roots

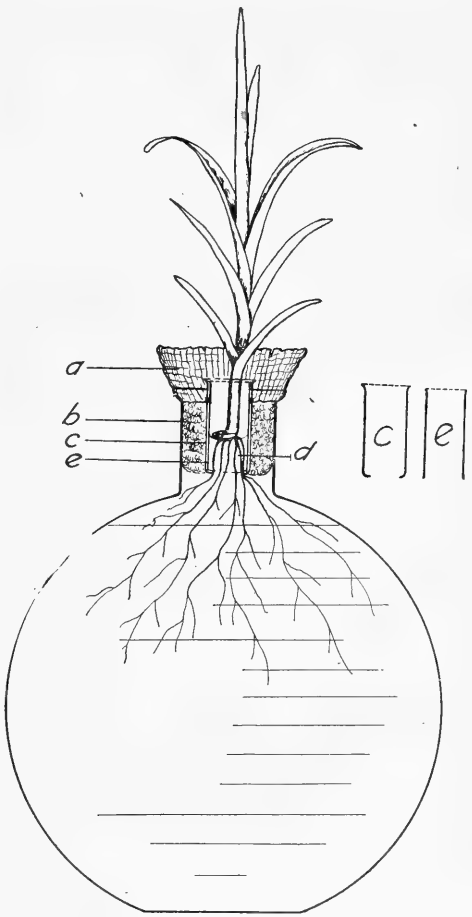

FIG. 1. DEVICE FOR GROWING LARGE PLANTS IN STERILE MEDIA

a, Cheesecloth; *b*, cotton wool; *c*, outside tube into which *e* slides; *d*, agar carried over from test tube with plantlet; *e*, tube in which seed germinates

had developed and passed thru the agar to the bottom of the glass tube, the plantlets were transferred. The tube (fig. 1, *e*), with agar and plantlets, was lifted out of the test tube and set into the mouth of the prepared flask. This was accomplished with sterile forceps.

PREPARATION OF THE FLASKS

The flasks used were in most cases of 8-liter capacity, altho some held 12 liters. As much of the nutrient solution was put into each flask as could be sterilized. A piece of cloth was stretched over the mouth, and a hole just large enough to permit the insertion of a piece of tubing from 28 to 30 millimeters long (fig. 1, *c*) was cut in the cloth. This tubing (*c*) was just large enough to allow the plant and its tubing (*e*), described above, to telescope into it.

The lower end of the tube (*c*) was slightly constricted, to prevent the inner tube (*e*) with the plant from going too far into the flask. Enough cotton (*b*) was wrapped around the tube to hold it firmly in place when it was pushed into the mouth of the flask. The upper end of the tubing was adjusted so that it came about even with the top of the flask. The lower end extended below the cotton and the cloth (*a*), so that when the flask was full of liquid the liquid would just touch the tubing but not the packing. Each flask was then covered with a large beaker. The inverted beaker was large enough to leave some space for the growing plant.

Since there was need for more solution in the flask than could be sterilized in it, an extra amount was prepared which could be poured thru the opening that was left.

NUTRIENT SOLUTION

The nutrient solution had the following composition:

Calcium nitrate, $Ca(NO_3)_2+4H_2O$	2.70 grams
Magnesium sulfate, $MgSO_4+7H_2O$	0.60 gram
Potassium chloride, KCl	0.75 gram
Potassium dihydrogen phosphate, KH_2PO_4	1.50 grams
Ferric sulfate, $Fe_2(SO_4)_3$	0.05 gram
Distilled water to make	1000 cubic centimeters

This was designated as the full nutrient solution. In most cases of actual use it was diluted to ten times this volume. In earlier work it had been noted that certain plants, especially maize, tend to become chlorotic

before maturity. By painting the blades with a ferric chloride solution, it was found that this chlorosis was due to a deficiency of available iron. Therefore about 0.5 gram of ferric phosphate was added to each container before sterilization.

SETTING OF THE PLANTS

Before the plantlets were set into the mouth of the flasks they were thoroly examined for contamination. Only the very best plantlets were used, and if properly handled they suffered no setback. In case the plantlets were large enough when placed in the flasks, they were wrapped in sterile cotton and the beaker was removed. In other cases several days were required for the plants to become large enough, and in this event the beaker was left on.

HARVESTING THE PLANTS

The plants were harvested in all stages of growth, as is shown by figures 5 to 9. The harvesting process consisted in bringing flask and plant to the laboratory, and, in most cases, first making a photograph and subsequently opening the flask by removing the plant and the cotton packing. When this was done the solution was examined for infection, which was determined by plating about 10, 5, 1/10, and 1/100 cubic centimeters. The medium used in the plates contained, in addition to peptone and beef extract, some form of sugar, usually glucose. The plates were incubated at from 20° to 25° C. for a week, or longer in case no infection was noted. The results reported in the subsequent data herein were obtained from the platings in which no infection was found, and these flasks were considered to be sterile.

ANALYSIS OF NUTRIENT SOLUTIONS AND RESIDUES IN BOTTOM OF FLASKS

The presence of nitrite nitrogen was determined by Ilosvay's modification of Griess' test, described by Treadwell (1915).

A qualitative test for the presence of nitrate nitrogen was made by the diphenylamine method (Withers and Ray, 1911). When it was present, the total quantity was determined by the phenoldisulfonic-acid method, slightly modified by the addition of 5 drops of a 0.5-per-cent solution of Na_2CO_3 before evaporating to avoid any loss of nitrogen which might be

FIG. 2. OAT PLANT GROWN IN STERILE SOLUTION FOR 105 DAYS

(Table 1, serial no. 1272)

present in the form of HNO_3. (The quantity of soluble organic matter in the plant solutions was not great enough to interfere with the proper nitration of the phenoldisulfonic acid.)

Ammonia was determined by direct nesslerization.

Organic nitrogen in the plant solutions was determined according to the method described by the American Public Health Association (1905).

The total organic matter in the solutions was determined by evaporating 100 cubic centimeters of the filtered solution and igniting the residue thus obtained at dull red heat. The loss on ignition was reported as organic matter.

The dry weight of the deposit in the bottom of each flask was ascertained by transferring it to a filter, drying it at 110° C., and weighing it, the weight of the dry filter being subtracted from the total weight.

The amount of organic nitrogen in the deposit in the bottom of each flask was found by transferring the filter and contents from the previous determination to a Kjeldahl flask, digesting by the Gunning method, neutralizing the excess acid with ammonia-free Na_2CO_3, and distilling off the ammonia, which was nesslerized.

TESTS FOR THE PRESENCE OF ORGANIC NITROGEN IN NUTRIENT SOLUTIONS IN WHICH PLANTS OF SEVERAL KINDS HAD GROWN

Several different kinds of seeds were germinated under aseptic conditions, and were transplanted, in the manner described, to flasks containing the usual nutrient solution of one-tenth strength. The manner of growth of the plants in these flasks is shown in figures 2 to 4.

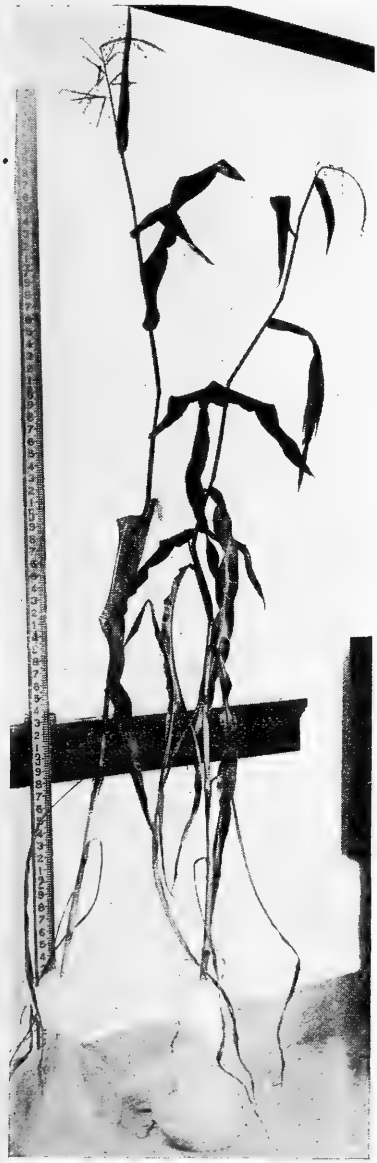

FIG. 3. MAIZE PLANTS GROWN IN STERILE SOLUTION FOR 189 DAYS
(Table 1, serial no. 1303)

FIG. 4. PEA PLANT GROWN IN STERILE SOLUTION FOR 139 DAYS
(Table 1, serial no. 1280)

In one flask the usual nutrient solution was not employed, as it was desired to ascertain whether a leguminous plant grown in a solution containing no nitrogen would liberate nitrogenous matter in the solution in appreciable quantities. The flask used for this purpose was pea flask no. 1302, in which the nutrient solution was composed of 1.5 grams KH_2PO_4, 1 gram $CaCl_2$, 0.07 gram Na_2SO_4, and 0.5 gram $Fe_2(PO_4)_2 + 8H_2O$; the flask was then filled with sterile tap water, the $Fe_2(PO_4)_2 + 8H_2O$ remaining largely undissolved.

After the contents of the flasks were sterilized and the young plants transferred, the cultures were taken to the greenhouse, where they remained for various periods. It was not intended to make any systematic study of the relation of the stage of growth to the quantity of organic nitrogen in the solution at harvest. This would have been impossible under the circumstances, for the plants were set out at different times and, since conditions affecting plant growth vary greatly in the greenhouse at different seasons of the year, no comparison of this kind could be attempted. The same difficulty would obtain in case a comparison of different plants was desired, except in the case of such plants as were placed in the greenhouse at about the same time.

When it was decided to harvest a plant, the flask was brought to the laboratory, and, after a photograph had been taken, the plant was removed from the nutrient solution and the dry matter and nitrogen were determined in the entire plant including the roots. A plating of the nutrient solution was made to determine whether the solution was sterile. The presence of any molds or bacteria thus detected excluded from the experiment the flask so contaminated.

The volume of liquid remaining in the flask was measured, and determinations were made of the nitrate nitrogen remaining in the solution, the ammonia nitrogen, if any, and the organic nitrogen present in soluble form. The deposit at the bottom of the flask was collected and a determination was made of the organic nitrogen contained in it. The reason for ascertaining the quantity of nitrate nitrogen remaining in the solution was merely to observe whether the presence or absence of this form of nitrogen affected the liberation of organic nitrogen by the plant.

A small quantity of nitrogen was contained in the germinated seed and plantlet placed in the flask, but there was no way by which this nitrogen

TABLE 1. FORMS AND AMOUNTS OF NITROGEN PRESENT IN SOLUTIONS IN WHICH PLANTS HAD GROWN

Kind of plant	Maize	Oat	Pea	Pea*	Maize	Vetch
Serial no.	1259	1272	1280	1302	1303	1308
Date of setting plant in flask	Dec. 1	Dec. 29	Dec. 9	Dec. 9	Dec. 1	Jan. 20
Date of removing plant from flask	April 1	April 11	April 26	April 26	June 7	June 12
Growing period (days)	122	105	139	139	189	144
Dry matter in plant (milligrams)	11,367.8	4,089.0	6,823.0	.....	48,490.0	18,050.0
Nitrogen in plant (milligrams)	248.9	151.0	231.5	43.6	472.3	344.9
Volume of solution at harvest (cubic centimeters)	9,850.0	7,320.0	4,510.0	6,815.0	6,950.0	2,290.0
Condition of solution	Sterile	Sterile	Sterile	*B. radicicola*	Sterile	Sterile
Nitrogen in solution at harvest in form of						
NO_3 (milligrams)	241.9	198.3	89.6	None	None	None
NH_3 (milligrams)	2.7	Trace	Trace	2.0	6.3	None
Organic matter (milligrams)	13.4	18.3	3.6	2.0	3.4	4.4
Organic nitrogen in deposit at bottom of flask (milligrams)	0.8	0.5	0.2	0.7	0.6	1.0

* The nutrient solution in which this pea plant was grown contained no combined nitrogen at the beginning of the experiment.

could be transferred to the nutrient solution except thru the roots, as the seed did not come in contact with the solution at any time.

The data for this experiment are presented in table 1. The figures give some definite information regarding the presence of organic nitrogen in the substratum in which these plants grew and which contained only inorganic nitrogen at the time when the young plants were set out. Of the plants used — oats, peas, maize, and vetch — all liberated organic nitrogen, which was found both in the solution and in the deposit at the bottom of the flasks. The quantity of organic nitrogen in the solution was always several times as much as that in the deposit.

The organic nitrogen in the deposit at the bottom of the flasks is probably the result of sloughing off of the root cells, as is indicated by the presence of plates of cells in the deposit. It is possible also that a part, at least, of the nitrogen in solution is liberated from the plant cells in the same way. There is no direct evidence that the nitrogenous matter is liberated in any other way, but it is perhaps questionable whether the quantity found in solution, especially during the early stages of growth, could all have come from detached cells. That these cells are alive and remain so for a considerable time has been noted by Knudson (1919).

Organic nitrogen appeared in the solution before the nitrates were all removed. It is evident that organic nitrogen is liberated by these plants in the early stages of their growth and not exclusively at the period between full bloom and maturity. That only the loss of nitrogen in later growth was noticed in the field experiments previously reviewed was doubtless due to the fact that the plants were absorbing little nitrogen at that stage and were liberating it more rapidly than they were absorbing it.

The quantity of organic nitrogen liberated under field conditions may not correspond to that obtained in these experiments, as under the conditions of the experiments there was no removal of organic matter by organisms other than the plant, while in the field there would presumably be conversion of the organic nitrogen into ammonia and nitrates.

The pea plant that grew in a solution without the addition of combined nitrogen, liberated organic nitrogen into the solution in which it grew. The growth was by no means as vigorous as that of the pea plant which was furnished with nitrate nitrogen, and the plant itself contained only about one-fifth as much nitrogen as did the other pea plant, but it liberated more than half as much organic nitrogen.

ORGANIC NITROGEN PRESENT IN NUTRIENT SOLUTIONS AT SUCCESSIVE STAGES IN THE GROWTH OF MAIZE

In order to ascertain how the stage of growth of maize plants affects the quantity of organic nitrogen found in the nutrient media, a series of flasks containing nutrient solution were prepared in the usual way and a young plant was set in each flask. The flasks were placed in the greenhouse on December 24, 1915. They were allowed to remain there until the time when they were to be brought to the laboratory for analysis of the plants and the contents of the flasks. The first flask was opened on March 4, 1916, and the others were opened at intervals of a number of days until May 24, 1916, when the last one was opened. The interval between the opening of the first and that of the last flask covers a period of growth between the pre-tassel stage and maturity (figs. 5 to 9).

The maize plants grew well and most of those that were old enough at harvest bore ears. The variety used was a pop corn which under normal conditions does not grow very tall. Data regarding all of the flasks the contents of which were sterile at harvest are given in table 2. All of the contaminated flasks except one were discarded in presenting the results. The one exception was made because it fell in what would otherwise have been a wide interval between the dates of harvest. It also represented the condition of most of the contaminated flasks, which did not appear to be materially different from the sterile flasks in respect to the quantity of organic nitrogen present in the nutrient solution.

The data in table 2 are consistent in showing the presence of organic nitrogen in all solutions in which plants grew. This organic nitrogen appeared at all stages in the growth of the plants, but there seemed to be a tendency for it to decrease in amount with progressive stages in the life of the plant, and especially about the time when the plant approached maturity, at which stage there was a very decided falling off in the quantity present.

The organic nitrogen in the deposit at the bottom of the flask did not show any decided tendency to vary in amount with the successive stages of plant growth. The amount present was uniformly smaller than that in the solution. In the bottom of the flask there could usually be found plant cells, indicating the sloughing off of root caps and root hairs. This suggests a possible source of at least a part of the organic nitrogen in

FIG. 5. MAIZE PLANT 71 DAYS OLD
(Table 2, serial no. 1246)

FIG. 6. MAIZE PLANT 82 DAYS OLD
(Table 2, serial no. 1250)

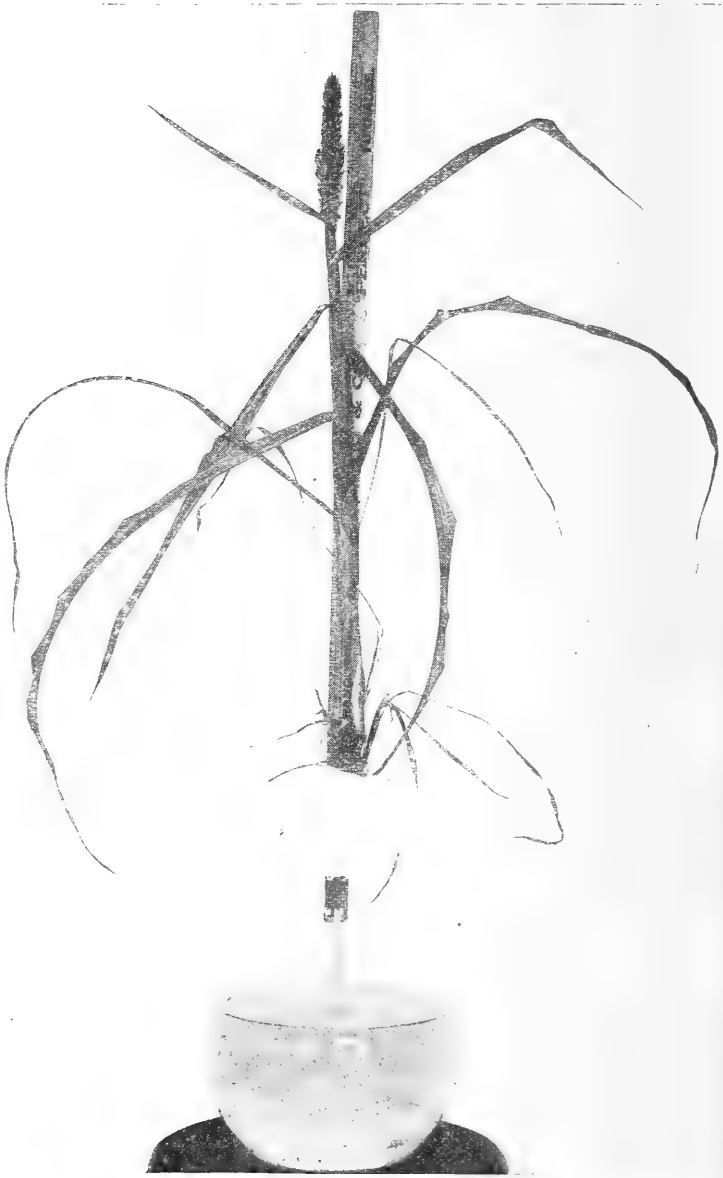

FIG. 7. MAIZE PLANT 91 DAYS OLD
(Table 2, serial no. 1253

FIG. 8. MAIZE PLANT 96 DAYS OLD
(Table 2, serial no. 1256)

FIG. 9. MAIZE PLANT 111 DAYS OLD
(Table 2, serial no. 1275)

TABLE 2. FORMS AND AMOUNTS OF NITROGEN PRESENT IN SOLUTIONS AT SUCCESSIVE STAGES IN THE GROWTH OF MAIZE

Kind of plant	Maize	Maize	Maize	Maize	Maize	Maize	Maize	Maize
Serial no	1246	1250	1253	1256	1275	1286	1291	1295
Date of setting plant in flask	Dec. 24	Dec. 24	Dec. 24	Dec. 24	Dec. 24	Dec. 24	Dec. 24	Dec. 24
Date of removing plant from flask	March 4	March15	March24	March29	April 14	May 3	May 17	May 24
Growing period (days)	71	82	91	96	111	130	144	151
Dry matter in plant (milligrams)	8,572.0	12,518.9	17,164.4	20,246.7	36,570.4	42,387.5	44,591.6	33,804.5
Nitrogen in plant (milligrams)	Lost	381.3	324.5	364.6	308.3	332.4	476.3	324.9
Volume of solution used by the plant (cubic centimeters)	1,370.0	2,040.0	2,500.0	2,960.0	5,705.0	6,455.0	8,240.0	5,710.0
Condition of solution	Sterile	Sterile	Sterile	Contaminated	Sterile	Sterile	Sterile	Sterile
Nitrogen in solution at harvest in form of								
NO_3 (milligrams)	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NH_3 (milligrams)	0.0	0.0	2.4	0.0	4.0	0.5	0.7	7.0
Organic matter (milligrams)	13.4	5.8	10.5	10.6	9.0	0.6	0.6	1.4
Organic nitrogen in deposit at bottom of flask (milligrams)	.....	0.9	1.2	0.6	0.9	Lost	0.4	1.0

solution and in the deposit, but whether it would account for all of the former may be questioned.

It was when the solution remaining in the flask was reduced to a rather small volume that the quantity of organic nitrogen in the solution fell decidedly. However, it did not appear that this was due to the saturation of the solution, as the large flask no. 1291, which contained 3700 cubic centimeters of solution at harvest, had no more organic nitrogen in the solution than did the smaller flask no. 1286, which contained only 1500 cubic centimeters of solution when opened.

It seems likely that the organic nitrogenous compounds are absorbed by the plant as it approaches maturity. This may be in order to establish equilibrium between the plant juices and the solution in which the roots are immersed. In the soil there would probably be a tendency for these organic nitrogenous compounds to undergo ammonification and nitrification, and, if conditions are favorable for these processes, there might be very little organic nitrogen in the soil solution at any time. Consequently, if there is a tendency to establish osmotic equilibrium there would probably be a much greater removal of organic nitrogen from a plant growing in soil than from one growing in a sterile solution.

Organic nitrogen appears in the nutrient solution before all of the nitrate nitrogen has disappeared, but the disappearance of nitrates is not a signal for the decided drop in organic nitrogen which occurs much later.

Previous investigations concerning the liberation of nitrogen from higher plants during growth have been conducted in two ways. One of these consisted in analyzing the plants from a measured area of land at certain intervals in the growth of the plants. Such experiments usually demonstrated that there was a loss of nitrogen from the plants between blossoming and ripening. Owing to the fact that the plants were absorbing nitrogen rapidly at earlier stages of growth, the income was greater than the outgo and consequently the earlier movement of nitrogen was not discovered. The other method, used by Le Clerc and Breazeale, in which the leaves were washed, showed a removal of nitrogen at each stage to which it was applied, but naturally the loss so occasioned would be rather small under natural conditions as it would occur only during periods of rainfall or heavy dew.

The movement of organic nitrogen from the plant into the soil solution ɔuld presumably be considerable, and possibly the cycle involving the sorption of nitrate nitrogen by the plant and its conversion into organic mpounds followed by a return to the soil of a part of these compounds d a reconversion of the nitrogen into nitrates may be a very extensive e. What part it may play in the economy of the plant is at present ly a matter of speculation. It may be that the liberation of this material merely casual, while, on the other hand, it is conceivable that the bstances so eliminated are more or less injurious to the plant and when posed to the decomposing bacteria of the soil are destroyed and not ıbsorbed. When liberated into a sterile solution they are not destroyed, d, being largely reabsorbed, they may exert a toxic effect on the plant, ıich never makes a perfectly healthy growth in these solutions even ıen it produces grain.

TOTAL ORGANIC MATTER PRESENT IN NUTRIENT SOLUTIONS IN WHICH MAIZE PLANTS HAD GROWN

The experiments previously described have dealt only with the forms nitrogen present in solutions in which higher plants have grown. It uld appear to be a matter of some interest to know something of the al quantity of organic matter in these solutions, and what proportion s organic matter may bear to the nitrogen present. For this purpose ıumber of flasks containing the usual nutrient solution of one-tenth ength were prepared and maize plants were grown in these in the tomary way. It was planned to have a set of four flasks to be opened er the plants had grown for about two months, and another set of the ıe number of plants to be harvested when fully mature. Unfortunately, flasks in the latter set were all found to be contaminated when ned, and for that reason the data furnished by these flasks are not sidered to be of value and are not included in table 3, which gives data for the first four flasks only:

TABLE 3. TOTAL ORGANIC MATTER AND NITROGEN PRESENT IN SOLUTIONS IN WHI MAIZE PLANTS HAD GROWN

Kind of plant	Maize	Maize	Maize	Ma
Serial no	1	2	3	
Date of setting plant in flask	May 1	May 1	May 1	May
Date of removing plant from flask	June 23	June 23	June 23	June
Growing period (days)	53	53	53	53
Dry matter in plant (milligrams)	17,266.4	23,076.4	24,058.5	20,443.
Nitrogen in plant (milligrams)	357.1	327.4	400.0	365.
Volume of solution at harvest (cubic centimeters)	5,875.0	4,155.0	3,855.0	4,870.
Condition of solution	Sterile	Sterile	Sterile	Steri
Total organic matter in solution at harvest (milligrams)	466.6	353.1	476.1	535.
Nitrogen in solution at harvest in form of				
NO_3 (milligrams)	0.0	0.0	0.0	0.
NH_3 (milligrams)	0.0	0.0	0.0	0.
Organic matter (milligrams)	1.7	1.0	1.3	1.
Ratio of organic matter in solution to dry matter in plant	1:37.0	1:65.3	1:50.5	1:38.
Organic nitrogen in deposit (milligrams)	0.0	0.4	0.8	0.
Nitrogen in organic matter in solution (per cent)	0.35	0.27	0.27	0.

The plants used in this experiment made a rather rapid growth, t conditions in the greenhouse during May and June being very favoral for the growth of maize. Not only had all of the nitrate and ammor nitrogen disappeared from the solution, but the organic nitrogen h been reduced to a very small quantity, being, in fact, lower than in a of the other experiments of this kind. It was rather surprising under t circumstances to find so much total organic matter in the solution. E dently but a small proportion of the organic matter present was of nitrogenous character, as the percentage of nitrogen in the organic mat in solution is only about 0.3. Probably there was much carbohydr material present. Knudson's (1920) investigations led him to conclu that reducing sugars are excreted by plant roots. Calculating the nitr enous organic matter at 6.25 times the nitrogen present, such mate would constitute only about one-fifth of the total organic matter. It altogether likely that the proportion of nitrogen in the organic mat varies at different stages in the growth of the plant.

The ratio of the organic matter in the solution to the dry matter in plant is surprisingly high. This varied from one part in the solution

7 parts in the plant, which was the narrowest ratio, to one part in the lution to 65.3 parts in the plant, which was the widest ratio. If it is be assumed that the decomposition of this organic matter in the soil ould increase its liberation by the plant, the result would be that a very rge quantity of organic matter would be transferred to the soil. It is ıtirely conceivable that higher plants may influence bacterial activity the soil by means of this liberation of organic matter, which would rnish a source of energy for certain bacteria, as, for instance, nitrate nsumers.

In the solutions in which these four plants grew there were at harvest ammonia, no nitrates, and very little organic nitrogen, which condition dicates a strong demand for nitrogen by the plants. Sometimes mmoniacal nitrogen was found to be present in the solutions and some- nes it was absent. The cause of its formation is an unsolved problem. wo possibilities present themselves. One is that ammonification of the ganic matter in the solution took place between the time when the sk was opened and the time when the test for ammonia was made, ntamination of the solution from outside occurring after the flask was ened. This was guarded against as far as possible. Another hypoth- s is that ammonia formation was due to enzymic action, the plants ving liberated the necessary enzymes.

Possibly ammonia is commonly formed and when the demand of the ants for nitrogen is great it is absorbed and thus disappears from the ution. If it is derived from the liberated organic nitrogen, as seems ssible, it may be the means by which organic nitrogen is rendered ailable to higher plants.

In a previous experiment, flasks were opened at four different stages in e growth of maize. As the periods of growth varied from a rather ly stage, before the nitrate nitrogen was all removed from the solution, maturity, it would have been a very interesting experiment had it not en for the fact that the last two flasks opened were found to be con- ninated. The data, however, are all tabulated in table 4, altho there of course, no assurance that the results were not materially affected the organisms that had gained access to the solutions.

The sterile flasks in this experiment agree with those in the experiment orded in table 3 in showing the presence of a large amount of organic tter in the solution in which the plants grew. The amount was less

for the data shown in table 4, but the growth of the maize plants in the sterile flasks also was less. The quantity of inorganic matter and of organic matter appears to decrease and increase at the same periods if credence is to be given to the data from the last two flasks opened. The

TABLE 4. TOTAL ORGANIC MATTER AND NITROGEN PRESENT IN SOLUTIONS AT SUCCESSIVE STAGES IN THE GROWTH OF MAIZE

Kind of plant	Maize	Maize	Maize	Maize
Serial no.	1	2	3	4
Date of setting plant in flask	June 28	June 28	June 28	June 28
Date of removing plant from flask	Aug. 3	Aug. 16	Aug. 30	Sept. 20
Growing period (days)	36	49	63	84
Dry matter in plant (milligrams)	10,200.0	24,100.0	32,200.0	65,000.0
Volume of solution at harvest (cubic centimeters)	6,200.0	6,950.0	2,850.0	2,790.0
Condition of solution	Sterile	Sterile	Contaminated	Mold
Nitrogen as nitrates in solution (milligrams)	32.4	Trace	0.0	0.0
Inorganic matter in solution (milligrams)	1,333.0	1,056.4	310.6	460.8
Organic matter in solution (milligrams)	291.4	284.9	76.9	251.3

data for inorganic matter were probably not influenced by the infection of flask no. 3, and this shows a gradual decrease in amount up to the sixty-third day of growth and then an increase at maturity, indicating a liberation of salts from the plant. Such liberation must, of course, have been by way of the roots. Admitting, then, that inorganic matter may be removed by the action of rainfall on the leaves, of which the investigations of Le Clerc and Breazeale leave little doubt, there appear to be at least two means by which this material may be liberated by the plant.

REDUCING AND OXIDIZING SUBSTANCES LIBERATED BY PLANT ROOTS

While many investigations have been made of the oxidizing and reducing enzymes in plants, very few have been undertaken for the purpose of ascertaining whether any of these bodies appear in the substratum in which the roots of plants are immersed. It was thought that the sterile solutions used in the experiments described above, in which plants of different kinds and of different stages of growth were produced, would permit of a series of tests for these substances under conditions that would exclude contamination from the seed or from outside sources

nd that these tests might possibly afford some information regarding he relation of the stage of growth of the plants to the presence of oxidizing r reducing substances.

REVIEW OF LITERATURE

Apparently the only examinations designed to detect the presence of educing substances in media in which plants grew were those conducted y Schreiner and Sullivan (1910), who placed the roots, and in some ases the seeds also, of wheat seedlings in solutions of various reagents ommonly used for detecting the presence of reducing substances. Conidering only the tests in which roots alone were introduced into the eagent solution, these authors obtained reactions with starch-iodide olution, sodium selenite, and sodium tellurite. Tests for reduction of itrates appear to have been made only where the seeds were present, nd under these conditions nitrites were found by means of the Griess eaction. The seeds from which the seedlings were germinated had reviously been treated with a 0.1-per-cent solution of mercuric chloride. he solutions in which the plants grew were not shown to be sterile.

It is well known that oxidizing enzymes occur within plant tissues nd they are believed to play an important part in physiological processes. hey have been found also in soils, but this does not furnish any proof iat they are liberated by plant roots altho it suggests such a possibility. he presence in soils of large numbers of bacteria many of which are nown to secrete enzymes, may well account for the appearance in soils oxidizing enzymes without any contribution from roots of higher plants. is equally true that the occurrence of enzymes within the plant would ot necessarily lead to the conclusion that they are thus conveyed to the oil.

Not many investigators have taken up studies concerning the liberation oxidizing substances by plant roots. The work of Molisch, Czapek, id Raciborski has been reviewed by Schreiner and Reed (1909), and ence it is not necessary to review it here. Schreiner and Reed, in the aper referred to, state that they have been able to detect the presence oxidizing enzymes on certain parts of the surface of wheat roots. For is purpose they used alpha-naphthylamine, benzidine, vanillin, vanillic id, phenolphthalin, aloin, and leuco-rosolic acid. As in their experiments r the detection of reducing substances, there was no evidence offered

to show that the solutions were sterile, but the authors state that it improbable that the enzymes were produced by bacteria.

Summarizing the experiments to determine the presence of oxidizi enzymes outside of the growing roots of plants, it may be said that Molisc Raciborski, and Schreiner and Reed report the finding of these enzym and consider them to have been excreted by the roots as a normal co dition of their growth. Evidence of the liberation of reducing substanc is less conclusive, but if oxidizing enzymes are liberated by plant roo it is easily conceivable that reducing substances would be also, as bo are well known to occur within the plant tissues.

TESTS FOR REDUCING AND OXIDIZING SUBSTANCES LIBERATED BY PLANT ROOTS

The data already presented show that a comparatively large amou of soluble organic matter may be given off by plant roots during t growing period. This organic matter may be derived in part from ro caps and root hairs that are sloughed off by plant roots as developme proceeds. The roots or detached cells may give up to the surroundi medium certain specific compounds, some of which may be enzymic character. In order to obtain information on this subject a number tests were made to detect the presence of certain substances that mig influence reduction or oxidation.

Reducing substances

A number of reagents that had been proposed for the detection of t presence of reducing substances were used for testing the solutions which maize plants had grown, and at the same time for testing che solutions consisting of the nutrient solution made up as it was for t growth of the maize plants. In some cases the solutions in which the pla had grown were boiled before being tested, but an unboiled portion w always tested at the same time. Some of the reagents failed to gi a reaction with any of the solutions tested and were discarded. Th were methylene blue, methyl violet, gentian violet, sodium selenite, a sodium tellurite. These failures may mean merely that the conditi under which their reactions occur did not obtain altho reducing substan may have been present.

Tests for reducing substances were made with prussian blue in solutions
om six sterile flasks in which maize plants had grown, using both the
boiled and the boiled samples of the solutions as well as check nutrient
lutions. These tests were made in solutions taken from plants at
ferent stages of growth. Ten cubic centimeters of each solution was
ed, and each received two drops of a 0.5-per-cent solution of phenol.
ter the prussian blue was added, the tubes containing the solutions were
owed to stand for twenty-four hours, at the end of which time notes
re taken on the results. In each of the six tests the unboiled solution
which the plant had grown gave a distinct reaction for reducing sub-
nces. The boiled solution gave no reaction in three tests, while in
e other three the result was rather uncertain. The check solution
ve no definite test for reducing substances.

Reduction of nitrates.— Since traces of ammonia were found in the
rile solution which had surrounded the maize roots, it was thought
ssible that thru the action of enzymes liberated by the plant this
monia might have been formed from the nitrates in the nutrient solution.
sts for nitrates were made, using sulfanilic acid and naphthylamine
tate. No positive results were obtained. As a further test the
henylamine reagent was employed. This reagent is considered to be
sitive to nitrite 1 part in 32,000,000 and to nitrate 1 part in 44,000,000.
e tests were made with a series of sixteen flasks and no positive results
re obtained.

This does not necessarily show, however, that reducing enzymes might
have been present, for the maize removed all the nitrates from the
rient solution rather early in its development, and the liberation of
ucing substances may not occur until after the plant has taken up most
the nutrients necessary for its development, or the nitrites may be
orbed by the plant.

The nitrites might not have been present because there were no nitrates
n which they could be formed. The problem of supplying the nitrates
l making the nitrite test was conducted as follows: Check flasks,
lve in number, were prepared with the same nutrient solution that
used for growing plants. A like number of test flasks were used
ch contained solution from around the plant roots. One hundred
ic centimeters was used in each flask, and the nitrate content was
le equal in both check and test flasks. The flasks received phenol

to make the concentration 1 to 500, and were placed in the incubat at 23° C. The next morning tests were made for nitrites, using the Grie reagent. No visible differences were apparent. A second test for nitrit was made after forty-eight hours. The result was positive in eve case. This test was repeated with the solution from another flask which a maize plant had grown. While not so striking, the results this case were also positive. Some tests were negative. A differen of NO_3 readings was not detectable in a colorimeter.

Another series of tests for nitrate reduction was conducted, using cubic centimeters of the solutions in which maize plants had grown f periods of varying lengths and adding to this a small quantity of calci nitrate solution, at the same time introducing two drops of a 0.5-per-ce solution of phenol. Alpha-napthylamine and sulfanilic acid were us to test for the presence of nitrites, the solutions being allowed to sta for certain lengths of time varying from two hours to three days. Su tests were made of the sterile solutions from eight flasks in which pla had been grown, the solutions being taken for the tests within a few minu after the flasks were opened. A sample of the solution from each of flasks except one was boiled before being tested, and another sample w not so treated. The check nutrient solution was tested in each ca Of the eight flasks tested, the unboiled solutions showed the presence nitrites in every case but one, the check solution showed the absence nitrites in six cases out of eight, and the boiled solution gave a react for nitrites in six tests but did not color so rapidly as did the unboil Apparently nitrate-reducing substances were usually present in unboiled solutions in which the maize plants had grown, and boiling solutions failed to render these substances incapable of bringing ab reduction of nitrates in the presence of phenol.

While the process of boiling did not completely prevent the lic surrounding the plant roots from effecting reduction of nitrates, it seer to curtail its activity, as is indicated by the slower coloration of the reac with the alpha-napthylamine and sulfanilic acid. The tests for redu substances by means of prussian blue, on the other hand, did not any more reaction with the boiled solutions than with the checks. Wh therefore, the operation of boiling produced some effects correspon to what might be expected from enzymes, there is some question a

whether the reducing substances were of that nature in view of the results with reduction of nitrates.

Oxidizing substances

Peroxidases were detected in the culture solution in which the roots of maize, vetch, oats, peas, soybeans, alfalfa, and timothy had grown. From 8 to 10 cubic centimeters of each solution was placed in a dry test tube together with a few drops of hydrogen peroxide. This was allowed to stand for from two to three minutes, and then from two to three drops of a 5-per-cent phenol solution were added. The latter was then followed by an alcoholic solution of guaiac. It was considered that a positive test was recorded if the color became blue in thirty minutes. With this test no difficulty was experienced in obtaining a reaction with solutions from all of the flasks tested. Boiled solutions treated likewise gave no reactions.

In working with the solution in which vetch roots had grown, a very strong reaction was obtained by the use of hydrogen peroxide and phenol. The solution was placed in dry test tubes and a few drops of hydrogen peroxide were added. This was allowed to stand at room temperature. After from three to four minutes a few drops of a 5-per-cent phenol solution were run down the side of the test tube. Shortly after contact of the materials, a growing yellow color developed, which gradually increased and on long standing settled out. This test was negative when the same solution was boiled. An extract of macerated vetch roots and nodules gave the same test. If this material was boiled, however, no reaction was obtained.

Phenolpthalin was used as a reagent for indicating the presence of oxidizing substances in the solutions in which maize plants had grown. For these tests both boiled and unboiled samples of the solutions were used. Checks consisting of the nutrient solution in which no plants had grown were also included. Phenol was added, as in the previous tests. Results from these tests were usually negative.

Experiments in which guaiac were used without a peroxide indicated the presence of an oxidase in solutions in which maize plants had grown only when the plants were very young. Agar in which timothy plants were grown always gave a reaction with guaiac.

Tests with pyrogallol included only one sterile flask. No phenol was used. At the end of one-half hour the boiled solution was clear, the

unboiled was brown, and the check was a light yellow. On the whole the tests for oxidizing substances cannot be said to have offered very strong evidence of their presence except in the case of peroxidases.

Possible coexistence of oxidizing and reducing substances

Altho the number of tests for oxidizing enzymes were rather few, reactions indicating their presence were confined mainly to the solutions from flasks which gave no marked response to tests for reducing substances. It seems likely that both classes of substances are coexistent in solutions in which plants are growing, and that at one time the oxidizing substances may be dominant and at another the reducing substances. Differences in the intensities of the reactions at various times may thus be accounted for. Apparently with the maize plant the predominating reaction was for reducing substances thruout most of the stages of growth.

It would appear from these experiments that some form of reducing substance is always present in the solutions in which plants are growing. Whether oxidizing substances are always present, it is more difficult to say. They were found in some of the solutions taken from flasks in which the plants had reached only an early stage of growth, and unless they are destroyed later on they must be present thruout the entire life of the plant. In the natural soil solution, enzymes might be destroyed and thus removed from active operation except when freshly liberated.

Nature of oxidizing and reducing substances

Boiling the solutions in which plants had grown completely terminated the activities of the oxidases, as was to be expected. It did not always have that effect on the reducing substances, especially the nitrate reducers. There would thus seem to be considerable doubt as to whether the reducing substances were enzymic in character, but they at least had the power of bringing about reduction of nitrates in the absence of bacteria.

SUMMARY

Plants were grown with their roots in large flasks (8 or 12 liters capacity) containing a nutrient solution, the entire contents of the flasks being sterile. At various stages in the growth of the plants they were removed from the flasks and analyzed for nitrogen, and the nutrient solution was

ested for sterility and analyzed for nitrates, nitrites, ammonia, and rganic nitrogen, and in some cases for total organic matter. A determiation of organic nitrogen in the deposit at the bottom of the flasks was lso made.

The plants grown were maize, oats, peas, and vetch. The nutrient olutions in which each of these plants grew contained nitrogen only n the form of nitrate when the plants were set in the flasks, but when the lants had grown for several weeks there was always organic nitrogen resent. Even before the nitrate nitrogen had all been absorbed by the lants, organic nitrogen appeared in the solutions.

The deposit at the bottom of each flask contained a small quantity f organic nitrogen, which was probably derived from sloughing off of the oot cells as indicated by the presence of plates of cells in the deposit. here was no direct evidence that the organic nitrogen in solution was berated in any other way, but it is questionable whether such a large uantity could all come from these cells, especially during the early stages growth.

A pea plant which grew in a solution without the addition of combined trogen liberated organic nitrogen into the solution in which it grew. he growth was by no means as vigorous as that of another pea plant hich was furnished with nitrate nitrogen, and the plant itself contained nly about one-fifth as much nitrogen as did the latter plant, but it berated more than half as much organic nitrogen.

A series of flasks in which maize was growing were harvested at successive ages in the growth of that plant, and the plant and the flask contents ere examined in the manner already described. Organic nitrogen peared in the solutions at all stages in the growth of the plants, but ere seemed to be a tendency for it to decrease in amount with proessive stages in the life of the plant and especially as the plant closely proached maturity. The organic nitrogen in the deposit at the bottom the flasks did not show any decided tendency to vary in amount with e successive stages of plant growth.

Determinations of total organic matter were made in the solutions om some of the flasks. This constituent was very large in amount compared with the nitrogenous organic matter present. Apparently ere was much non-nitrogenous organic matter in the solutions. Calcuing the nitrogenous organic matter at 6.25 times the nitrogen present,

this material would constitute only a small part of the total organi matter.

The presence of reducing substances in solutions in which plants ha grown was indicated by certain tests, but a number of other reagent failed to give reactions. Nitrates were nearly always reduced in thes solutions in the presence of an antiseptic. Boiling the solution did no entirely prevent nitrate reduction, but it greatly decreased the rate a which reduction proceeded.

Peroxidases were always present in solutions in which plants had grow Boiling these solutions caused them to give no reaction for peroxidase Tests for other oxidizing substances were not sufficiently satisfactory t warrant the conclusion that they were present.

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LYSIMETER EXPERIMENTS—II

RECORDS FOR TANKS 13 TO 16 DURING THE YEARS 1913 TO 1917 INCLUSIVE

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RECORDS FOR TANKS 13 TO 16 DURING THE YEARS 1913 TO 1917 INCLUSIVE

T. Lyttleton Lyon and James A. Bizzell

The object of the experiments herein described was, in the main, similar to that of the lysimeter experiments previously reported by the authors,[1] the essential differences being that a soil of another series was used, and that the effect of different cropping systems on the removal of the soil constituents in the drainage water was not a feature of the present experiment. The lysimeter tanks were like those described in the earlier publication.

THE SOIL USED

The tanks were filled in the summer of 1910 with a soil classified by the United States Bureau of Soils as Volusia silt loam. The soil is typical of much of the hill land of southern New York. It was formed, in the main, from shale and sandstone as the result of glaciation, which was rather feeble on these high lands. There is much broken shale distributed thru the soil, the pieces varying in size from small particles to large rocks. The subsoil is often very compact, and even on the hillsides poor drainage is the rule. The soil layer is often shallow on the hills, the shale in some places lying three or four feet below the surface.

In chemical composition this soil is distinguished by its low content of calcium. The other soil constituents are present in what may be considered fairly liberal quantities. Agriculturally Volusia silt loam ranks as poor, and the sample placed in these lysimeter tanks is considerably less productive than the average soil of the type. It is a much less productive soil than the Dunkirk clay loam contained in tanks 1 to 12. Its low productivity as a type may be due in part to its location, which is mainly on high elevations, the approaches to which are steep, making it inaccessible to railroads and thus adding to the difficulty of applying lime and fertilizers, which have consequently been meagerly used on these lands.

[1] Lyon, T. Lyttleton, and Bizzell, James A. Lysimeter experiments. Records for tanks 1 to 12 during the years 1910 to 1914 inclusive. Cornell Univ. Agr. Exp. Sta. Memoir 12:11–15. 1918.

Acknowledgment.— The authors wish to express their thanks to Mr. E. W. Leland for his services in measuring and sampling the drainage water during the entire period of the experiments, and for supervising the cultural operations on the tanks.

Volume weight

Before the soil was placed in the tanks all stones larger than a walnut were removed from it, but, as is characteristic of this soil series, a large number of small stones still remained. It is probably on this account that the volume weight of the soil was so high. The weight of each twelve-inch layer of air-dry soil placed in the tanks is shown in table 1:

TABLE 1. AVERAGE WEIGHT OF EACH TWELVE-INCH LAYER OF SOIL IN TANKS

	First foot (pounds)	Second foot (pounds)	Third foot (pounds)	Fourth foot (pounds)
Weight of soil in tanks	2,250	2,170	1,850	1,75
Weight of soil per acre	5,625,000	5,425,000	4,625,000	4,375,00

This, it may be remarked, is a soil having greater volume weight than the Dunkirk clay loam used in tanks 1 to 12 inclusive, owing, in part at least, to the large number of stones.

Mechanical composition

A statement of the mechanical analysis of the soil by the centrifuga method, including all particles from fine gravel to clay, is given in table 2

TABLE 2. MECHANICAL COMPOSITION OF SOIL IN FIELD FROM WHICH TANKS 13 TO 1 WERE FILLED

Separates	First foot (per cent)	Second foot (per cent)	Third foot (per cent)	Fourth foot (per cent
Fine gravel	2.32	5.32	3.00	5.1
Coarse sand	2.91	4.83	2.78	5.2
Medium sand	3.02	4.64	2.85	5.1
Fine sand	6.32	8.60	6.30	9.1
Very fine sand	15.92	18.22	15.80	14.7
Silt	50.88	42.60	51.25	39.9
Clay	18.63	16.79	18.02	20.6

This soil has always permitted the rainfall to percolate readily since t has been in the tanks. At no time has there been any stoppage and there ıas never been any water standing on the surface. The soil has, on the vhole, drained more quickly and given a clearer percolate than did the Dunkirk clay loam in tanks 1 to 12.

Chemical composition

The samples used for the mechanical analysis of the soil in these tanks vere taken from each foot layer and represent the average composition of the four tanks. The samples for the chemical analysis were obtained in he same manner. Bulk analyses were made. The methods used are tated in the appendix to Memoir 12 (pages 85 to 87) and the results are given in table 3:

TABLE 3. CHEMICAL ANALYSIS OF SOIL PLACED IN TANKS 13 TO 16

Constituents determined	First foot	Second foot	Third foot	Fourth foot
Nitrogen (per cent)	0.145	0.052	0.059	0.050
Organic carbon (per cent)	1.560	0.270	0.115	0.080
Calcium oxide (per cent)	0.230	0.165	0.260	0.365
Magnesium oxide (per cent)	0.560	0.390	0.290	0.460
Potassium oxide (per cent)	1.690	1.810	1.710	2.170
Sodium oxide (per cent)	1.120	0.940	0.810	1.070
Phosphoric anhydride (per cent)	0.071	0.039	0.018	0.071
Sulfur trioxide (per cent)	0.042	0.033	0.041	0.031
Carbon dioxide as carbonate (per cent)	0.030	0.030	0.020	Trace
Lime requirement (CaO in parts per million)	1,350	800	650	400

The chemical analysis shows a relatively good supply of plant nutrients s compared with the average soil or with the Dunkirk soil in tanks 1 o 12, but the Dunkirk is a much more productive soil, as is evident on omparison of the yields of crops from both sets of tanks. The only lements in which the surface foot of the Volusia soil is materially below hat of the Dunkirk are calcium and sulfur. Nitrogen, phosphorus, nd potassium are about equal in amount in the two surface soils. The me requirement according to the Veitch method is somewhat greater ı the Volusia soil. In the second, third, and fourth feet the calcium is

much higher in the Dunkirk soil. If the difference in productiveness and other properties is to be traced to any difference in chemical composition, it would appear that calcium and possibly sulfur are the only constituents that would call for inspection. It is true, however, that magnesium is higher in the surface foot of the Volusia soil.

MANURE AND FERTILIZERS USED

Farm manure was applied once to the soil in each of the four tanks. This application was made in the spring of 1914. The analysis of the manure is given in table 4. The method of analysis is described in the appendix to Memoir 12, pages 90 and 91.

TABLE 4. Composition of Farm Manure Applied to the Soil in Tanks 13 to 16

Constituents	Percentage composition	Pounds per acre
Dry matter	21.26	4,252
Nitrogen	0.50	100
Phosphoric anhydride	0.37	74
Potassium oxide	0.36	72
Calcium oxide	0.63	126
Magnesium oxide	0.27	54

The burnt lime, of which one application was made, contained 91.95 per cent of CaO and a trace only of MgO.

METHODS FOR CHEMICAL AND MECHANICAL ANALYSES

The methods used for the chemical analyses of the soil, crops, drainage water, rain water, manure, lime, and potassium sulfate, and for the mechanical analysis of the soil, are described in the appendix to Memoir 12, pages 85 to 91, inclusive.

SOIL TREATMENT AND CROPPING SYSTEM

The four tanks used in this experiment were all filled in the late summer of 1910. From that time until the spring of 1913 they were not treated in any way, but the drainage was collected, measured, and analyzed in

order to have a complete record of all constituents removed in the drainage water from the time when the soil samples were taken for analysis. Since the present report does not attempt to show the difference in the composition of the soil at a later period, but is rather a discussion of the effect of the application of burnt lime on the composition of the drainage water and the plant ash, the drainage for the period previous to May 1, 1913, is not considered.

Farm manure was applied to each of the four tanks in the spring of 1913, the application being at the rate of 10 tons to the acre. Burnt lime was applied to tanks 15 and 16 in the spring of 1913 at the rate of 3000 pounds to the acre.

Tanks 14 and 16 were never planted to any crop, and growth of vegetation on them was prevented by hoeing. In the year 1915, when maize was growing on tanks 13 and 15, the unplanted tanks were hoed at the same time and in the same way as were the tanks planted to maize; when other crops were growing on the planted tanks, the unplanted ones were merely scraped with a hoe. In each tank planted to maize there were eighteen maize plants. Seven rows of oats and the same number of rows of barley were sown in each tank planted to those crops. The barley was used to replace wheat, which had been sown in the previous autumn and had winterkilled. Canada peas were planted broadcast. All crops grew to maturity and produced seed, but it was evident that the soil was not a very productive one. The manure, lime, and crop treatments are shown in table 5:

TABLE 5. SOIL TREATMENT AND CROPS RAISED ON LYSIMETER TANKS 13 TO 16 DURING THE PERIOD FROM 1913 TO 1917

Tank	Soil treatment		Crops raised				
	Fertilizer	Lime	1913	1914	1915	1916	1917
3	Farm manure	None	Oats	Canada peas	Maize	Oats	Barley
4	Farm manure	None	None	None	None	None	None
5	Farm manure	Burnt lime	Oats	Canada peas	Maize	Oats	Barley
6	Farm manure	Burnt lime	None	None	None	None	None

QUANTITY AND RATE OF PERCOLATION

The rainfall that percolated thru the soil was measured by monthly periods, and a record of each tank by months is therefore available. It is thus possible to ascertain the effect of certain treatments, such as liming and cropping, on the proportion of the rainfall passing thru the soil, and even to compare the relative permeability of the two soils.

Percentage percolation of rainfall

The figures for the flow of drainage water from each of the lysimeter tanks 13 to 16, expressed in liters for each month from May 1, 1913, to April 30, 1918, are given in table 2 of the appendix (pages 78 to 80). The flow calculated to acre inches annually for the same period is given in table 3 of the appendix (page 80). These tables furnish the data from which the average annual percolation in inches from the unplanted soil may be found, and also that from the soil on which crops grew. This, together with the percentage percolation, is given in table 6. The rainfall during the five-years period averaged 32.97 inches annually.

TABLE 6. Average Annual Percolation of Rainfall from Unplanted and from Planted Soil during Five-Years Period

Tanks	Crop treatment	Average annual percolation	
		Inches	Per cent of rainfall
14, 16	No plants allowed to grow	27.13	82.3
13, 15	Plants raised every year	20.62	62.5
	Difference in percolation	6.51	19.8

On the basis of these figures, about four-fifths of the rainfall percolated thru the bare soil and three-fifths thru the cropped soil. Somewhat more than one-fifth of the rainfall may therefore be considered as being used by the crops, since the evaporation from the surface of the unplanted soil may be assumed to be greater than that from the surface of the planted soil. This, however, is only a small proportion of the total rainfall and would account for only about six and one-half to seven inches of the annual precipitation.

Comparing the figures for percolation thru the Volusia soil with those thru the Dunkirk, given in the earlier publication already referred to, it will be seen that the former soil is more permeable than the latter and that the crops on the former used about an inch more rainfall.

In table 4 of the appendix (pages 81 to 83) are given the weather records at Ithaca by months, including the rainfall, the mean maximum, mean minimum, and mean temperatures, the hours of sunshine, the average hourly velocity of the wind, and the mean humidity of the air, for the period from May 1, 1913, to April 30, 1918.[2] These data were obtained at a distance of somewhat less than a mile from the lysimeters.

Effect of liming on percolation

As already stated, tanks 15 and 16 received an application of burnt lime at the rate of 3000 pounds to the acre. It has frequently been said that liming, especially with burnt lime, has a tendency to make a heavy soil more permeable to water. If such has been the effect of the lime on this soil, it may possibly be shown by comparing the volume of drainage water from the limed and the unlimed tanks. There may be some question, however, whether any flocculating action which the lime may have had on the upper six or seven inches of soil with which it was incorporated would increase the amount of percolation thru the entire four feet of soil. Comparisons would best be made between limed and unlimed tanks that have otherwise received similar treatment, and this is done in table 7. It is evident from this table that the application of lime has

TABLE 7. AVERAGE ANNUAL PERCOLATION OF RAINFALL THRU LIMED AND UNLIMED SOIL DURING FIVE-YEARS PERIOD

Crop treatment	Fertilization	Soil not limed		Soil limed	
		Tank	Flow (acre inches)	Tank	Flow (acre inches)
No plants allowed to grow.....	Farm manure.	14	28.60	16	25.66
Oats, peas, corn, oats, barley...	Farm manure.	13	21.28	15	19.96
Average.....			24.94		22.81

[2] The authors are indebted to Dr. W. M. Wilson for the weather records at Ithaca.

not caused a greater percolation of water. The same was true of the application of lime to the Dunkirk soil in tanks 1 to 12, in the earlier experiments. While this may not mean that the lime did not flocculate the upper layer of soil with which it was incorporated, it has some significance so far as drainage is concerned, since it indicates that liming a soil of this kind would not result in facilitating the removal of water thru tile drains.

WATER UTILIZATION BY CROPS

The water utilization by crops on this soil was large for the amount of dry matter produced, both when calculated to the minimum transpiration ratio and by the evapo-transpiration ratio. The former was calculated by subtracting the drainage from the planted tanks from the drainage from the unplanted ones, and amounts to 451 pounds of water for every pound of dry matter in the crops raised during the five-years period. This appears in tabular form in table 8:

TABLE 8. Minimum Transpiration for All Crops Raised during Five-Years Period

Tanks	Cropping treatment	Average annual percolation per tank (pounds)	Average annual production of dry matter per tank (pounds)
14, 16	Unplanted	2,462	.....
13, 15	Cropped	1,871	1.31
Minimum transpiration		591	.....
Minimum transpiration ratio		1:451	.....

Evapo-transpiration ratio

The evapo-transpiration ratio was calculated by subtracting the average percolation thru the planted tanks for the five-years period from the rainfall on the same area for the same period, and dividing this by the number of grams of dry matter per tank in the crops produced. This ratio is given in table 9:

TABLE 9. EVAPO-TRANSPIRATION FOR ALL CROPS RAISED DURING FIVE-YEARS PERIOD

	Liters per tank
Rainfall (average annual)	1,388.7
Percolation from planted tanks (average annual)	848.7
Transpiration and evaporation from planted tanks	540.0
Evapo-transpiration ratio	1:908

Neither the minimum transpiration ratio nor the evapo-transpiration ratio is necessarily the same as the actual transpiration ratio. The former is likely to be less because the evaporation from the unplanted soil is almost always greater than the evaporation from the planted soil, and the latter is almost sure to be greater because it includes the water that evaporates from the surface of the soil as well as that which is transpired by the plants. The actual transpiration ratio therefore lies between 1:451 and 1:908.

It is significant that both transpiration ratios for the Volusia soil are so much wider than those for the Dunkirk soil, the former being about 56 per cent wider than the latter in both cases. It seems fair to assume that the actual transpiration ratio is correspondingly wider for the Volusia soil. Such differences cannot be attributed to conditions other than the soil, and probably arise from a difference in the concentration of the soil solution. The transpiration ratios are inversely proportional to the concentration of the drainage water and the crop yields from these two soils, as may be seen in table 10, the data in which are for the five-years periods already reported with the exception of the crop yields, which are for 1915, 1916, and 1917 only, since those were the only years in which the same crops were grown on both sets of tanks.

TABLE 10. RELATION OF TRANSPIRATION RATIOS, TOTAL SOLIDS IN DRAINAGE WATER, AND CROP YIELDS

	Minimum transpiration ratio	Evapo-transpiration ratio	Total solids in drainage of unplanted tanks (parts per million)	Crop yields in 1915–1917 (grams per tank)
Volusia silt loam	1:451	1:908	297.7	3,359.0
Dunkirk clay loam	1:290	1:580	401.5	6,478.3

It would appear from the data presented in table 10 that an economic utilization of water by the plant accompanies a high concentration of the water passing thru the soil, and that there is, moreover, a relation between the concentration of this water and the productive ability of the soil.

Moisture relations of crops

In table 11 is given a statement of the moisture relation of each crop grown on these tanks during the five years of the experiment. The

TABLE 11. MOISTURE RELATIONS OF CROPS ON TANKS 13 AND 15 DURING THE PERIOD FROM 1913 TO 1917

Year	Tanks	Crop	Minimum transpiration ratio	Evapo-transpiration ratio	Transpiration and evaporation (acre inches)	Dry matter in crops (pounds per acre)	Rainfall in percolate (per cent)
1913	13, 15	Oats	1:373	1:690	10.13	3,542	65.08
1914	13, 15	Canada peas	1:525	1:1005	14.08	3,316	54.31
1915	13, 15	Maize	1:332	1:613	12.68	4,977	64.49
1916	13, 15	Oats	1:366	1:1108	11.85	2,546	54.75
1917	13, 15	Barley	1:755	1:1618	13.06	1,858	69.80

minimum transpiration ratios for all these plants are higher than for the same plants grown on the Dunkirk soil, and the evapo-transpiration ratios also are higher. These discrepancies emphasize the futility of trying to determine a standard for the water requirements of plants when soil is used as the medium in which the plants are grown.

REMOVAL OF NITROGEN FROM THE SOIL IN DRAINAGE WATER AND IN CROPS

There are large differences between the planted and the unplanted tanks in respect to the nitrogen removed in the drainage water, the amount from the unplanted tanks being in all cases larger. Nitrogen in the drainage water was all in the form of nitrates. There are considerable differences in the quantities of nitrogen removed from any one tank from year to year. In the unplanted tanks these differences do not appear to be associated with any weather conditions shown in the monthly records. It is possible that conditions extending over shorter periods may have influenced the production of nitrates. In the case of the tanks filled with Dunkirk soil in the earlier experiments, the removal of nitrogen appeared to be influenced by the total yearly rainfall for the year beginning May 1, but this does not account so satisfactorily for the removal of nitrogen from the Volusia tanks. Future experiments may throw more light on these relations.

Effect of liming on removal of nitrogen in crops

One of the beneficial effects which lime frequently exerts on soil showing a lime requirement is to promote the formation of nitrates from organic nitrogenous compounds. Such action might be reflected in the nitrogen content of the drainage water or in the nitrogen removed in the crops.

The amount of nitrogen removed in the crops produced each year of the experiment is shown in table 12:

TABLE 12. NITROGEN IN CROPS, CALCULATED TO POUNDS PER ACRE BY YEARLY PERIODS

Tank	Burnt lime (pounds)	Nitrogen in crops (pounds per acre)					
		Oats 1913	Peas 1914	Maize 1915	Oats 1916	Barley 1917	Total
13	None	34.98	68.75	28.35	21.74	18.79	172.61
15	3,000	36.24	94.86	37.41	24.93	23.74	217.18

It is apparent from the data presented in table 12 that in every year the crops on the limed soil contained more nitrogen than did the crops on the soil that was not limed. This, of course, is not positive proof that lime increases the production of nitrates in this soil, as nitrogen may not be

an important factor in crop production; on the other hand, it may be significant, especially if it is supported by evidence drawn from the removal of nitrogen in the drainage water.

Effect of liming on removal of nitrogen in drainage water

The quantities of nitrate nitrogen removed in the drainage water of unplanted soil afford a better means of ascertaining whether liming increases nitrate formation than does the removal of nitrogen in crops. The data by years for the nitrogen in drainage water from unplanted soil are presented in table 13:

TABLE 13. NITROGEN IN DRAINAGE WATER OF UNPLANTED TANKS, CALCULATED TO POUNDS PER ACRE BY YEARLY PERIODS (MAY 1 TO APRIL 30)

Tank	Fertilizer	Burnt lime (pounds)	Nitrogen in drainage water (pounds per acre)					
			1913	1914	1915	1916	1917	Total
14.....	Manure..	None	73.41	34.21	49.31	34.47	38.71	230.11
16.....	Manure..	3,000	88.45	49.56	55.79	50.80	46.19	290.79

In each year the removal of nitrogen in the drainage water from the limed soil was greater than from the unlimed, which is very good evidence that the lime produced a condition more favorable to the production of nitrates. It may be remarked that the application of lime to the Dunkirk soil was not attended by any increase in the removal of nitrogen by the drainage water or by the crops. This difference in effect of lime is all the more striking inasmuch as the lime requirement of the surface foot of the Dunkirk soil is very little less than that of the Volusia. The percentage of calcium, however, is about one-third less in the surface foot of the Volusia. In this case the relative calcium content of the soil is a better guide to its need of lime for nitrification than is the lime requirement as determined by the Veitch method.

Effect of liming on removal of nitrogen in both drainage water and crops

While the nitrogen in the crops alone may not be an adequate guide to the effect of lime on the soil, the nitrogen in the crops added to that in the drainage water from the same tanks is perhaps somewhat more com-

prehensive. These data are given in table 14. It is apparent from this table that the application of lime to this soil results in an increased

TABLE 14. NITROGEN IN BOTH DRAINAGE WATER AND CROPS, CALCULATED TO POUNDS PER ACRE IN YEARLY PERIODS

Tank	Burnt lime (pounds)	Nitrogen in both drainage water and crops (pounds per acre)					
		Oats 1913	Peas 1914	Maize 1915	Oats 1916	Barley 1917	Total
13	None	46.03	74.47	44.78	26.96	23.51	215.75
15	3,000	57.46	114.16	51.67	28.81	28.10	280.20

removal of nitrogen in the combined crop and drainage water. There would seem to be little doubt, in view of the data presented in the last three tables, that the effect of lime on this soil is to increase nitrate formation.

RELATION OF DIFFERENT CROPS TO FORMATION OF NITRATES

It has been noted that the experiments with Dunkirk soil indicated certain rather definite relationships between certain kinds of plants and the formation of nitrates. A similar relationship appears to exist in the experiments with Volusia soil, as may be seen in the data given in table 15:

TABLE 15. AVAILABLE NITROGEN IN SOIL PRODUCING DIFFERENT CROPS, AS MEASURED BY THE NITROGEN OF THE CROP AND OF THE DRAINAGE WATER

(In pounds per acre)

Crop	Nitrogen in planted tanks (average of tanks 13 and 15)				Nitrogen in drainage water in bare tanks (average of tanks 14 and 16)	Excess (+) or deficiency (—) in planted tanks
	In drainage water	In tops	In roots*	Total		
Oats (1913)	16	35	12	63	81	—18
Peas (1914)	12	81	27	120	42	+78
Maize (1915)	15	32	11	58	52	+ 6
Oats (1916)	4	23	8	35	42	— 7
Barley (1917)	4	21	7	32	42	—10

* Estimated at one-third the quantity in tops.

Estimating the nitrogen in the roots of each crop to amount to one-third the quantity in the above-ground part, it will be seen that the nitrogen in the oat crop added to the nitrogen in the drainage water from the tanks on which that crop grew was less in amount than the nitrogen in the drainage water from the bare tanks for the same period. The same was true of barley, but it was not true of maize or of peas. The excess of nitrogen from the pea tanks can doubtless be ascribed to the nitrogen-fixing properties of *Bacillus radicicola* in the nodules of the pea roots. The excess nitrogen from the maize tanks must be ascribed to some different phenomenon. It has been suggested[3] that some plants have the property of depressing the formation of nitrates, and that certain plants possess this property to a greater degree than do others. The data here presented are in line with such an hypothesis.

REMOVAL OF CALCIUM

Calcium was removed in the drainage water to a much greater extent than was any other of the bases determined, but in relatively small amounts by the plants. A comparison of the calcium in the drainage water of the Dunkirk and Volusia soils shows that the latter lost more calcium by leaching than did the former, in spite of the fact that this soil contained only about two-thirds as much of that element as did the Dunkirk soil. On the other hand, the crops grown on the Volusia soil contained less calcium but the yield of crops was much smaller. The total removal of calcium from the Volusia soil, from both planted and unplanted tanks, was greater than that from the Dunkirk.

Effect of plant growth on removal of calcium

In the experiments with Dunkirk soil it was found that less calcium was removed from the planted soil in crop and drainage water combined than was found in the drainage alone from the unplanted soil. This is true also of the Volusia soil, as may be seen from table 16:

[3] Lyon, T. Lyttleton, and Bizzell, James A. Some relations of certain higher plants to the formation of nitrates in soils. Cornell Univ. Agr. Exp. Sta. Memoir 1:1-111. 1913.

TABLE 16. AVERAGE ANNUAL REMOVAL OF CALCIUM FROM PLANTED AND FROM UNPLANTED TANKS

(In pounds per acre)

Tanks	Soil treatment	Calcium removed in		Total calcium removed
		Drainage water	Crops	
13, 15	Planted	256.4	8.7	265.1
14, 16	Bare	351.4	.....	351.4
Calcium conserved by cropping				86.3

The process of cropping conserves the calcium in the soil even when the entire crop is removed. The reason for the greater removal of calcium from the uncropped soil may be found, in part at least, in the large formation and leaching of nitrates when plants are not present. In table 17 are shown the average quantities of nitrates found annually in the drainage water of the planted and the unplanted tanks.

TABLE 17. AVERAGE ANNUAL REMOVAL OF NITRATES IN DRAINAGE WATER FROM PLANTED AND FROM UNPLANTED TANKS

Tanks	Soil treatment	Nitrates removed (pounds per acre)
13, 15	Planted	47.0
14, 16	Bare	231.7

The nitrates in the drainage water from the cropped soil would account for only about 11.5 pounds of calcium, while the nitrates from the unplanted soil correspond to about 56.5 pounds of calcium which might be removed in the form of nitrate. This would still leave about 245 pounds of calcium that had been removed in the drainage water from the planted soil in some form other than nitrate, and about 285 pounds from the unplanted soil.

The concentration of calcium in the drainage water from the planted and from the unplanted soil shows little difference, but this is in the same order as its total removal. This may be seen in table 18, in which is stated in parts per million the average calcium content for the five-years period.

TABLE 18. Average Calcium Content of Drainage Water from Planted and from Unplanted Tanks

Tank	Soil treatment		Calcium (parts per million)	
	Crop	Lime	For each tank	Average for crop treatment
13	Planted	Not limed	52.3	54.4
15	Planted	Limed	56.6	
14	Bare	Not limed	49.9	58.9
16	Bare	Limed	68.0	

The greater loss of calcium from the unplanted soil was not due entirely to the greater percolation of water thru that soil, since in that case the concentration would not be greater. It would appear that the presence of a large amount of a strong acid, such as nitric acid, in the unplanted soil would explain the greater concentration of the calcium in the drainage water of that soil as compared with the weaker carbonic acid in the planted soil.

Effect of liming on removal of calcium

The application of burnt lime to the Dunkirk soil at the rate of 3000 pounds to the acre in the earlier experiments did not result in increasing the quantity of calcium in the drainage water or in the ash of the crops produced. A similar application to the Volusia soil in this experiment appears to have decreased the amount removed in both of these ways, as may be judged from the data presented in table 19:

TABLE 19. CALCIUM IN DRAINAGE WATER AND IN CROPS
(In pounds per acre, annual average)

Tank	Burnt lime (pounds)	Calcium in drainage water	Calcium in crops	Total calcium
13	None	257.6	7.46	265.1
14	None	319.4	.....	319.4
15	3,000	255.1	10.09	265.2
16	3,000	383.4	.....	383.4

The figures for average annual calcium removal for the entire five-years period, as given in table 19, show a very large increase in the quantity of calcium leached out of the bare limed soil as compared with that from the bare soil unlimed; they show also a moderate increase in the calcium contained in the crops, but they do not indicate any effect from the liming on the calcium leached from the cropped soil. The evidence, however, is in favor of the conclusion that liming increases the amount of soluble calcium in Volusia soil, while it has no such effect on Dunkirk soil. This is hardly to be accounted for by the absorbent properties of the soil for lime, since Volusia soil has a somewhat higher lime requirement than Dunkirk as determined by the Veitch method.

The concentration of calcium was appreciably greater in the drainage from the limed soil than in that from the unlimed soil, both when planted and when kept free of vegetation, as may be seen in table 18.

Liming to maintain the calcium content

The Volusia soil, altho low in calcium, is annually losing a large quantity in the drainage water, particularly from the unplanted soil. The removal of calcium in the ash of crops has been small as compared with that in the drainage water. If the loss of calcium from the limed soil were to be replaced, it would require an annual application of 536 pounds of pure burnt lime, or 957 pounds of pure limestone, to supply the uncropped soil, and 371 pounds of burnt lime, or 662 pounds of limestone, to supply the planted soil with calcium to the amount removed in the crops and in the drainage water.

REMOVAL OF MAGNESIUM

Magnesium was removed in much smaller quantity than was calcium, both in the drainage water and in the crops. In both ways the removal was less from the Volusia soil than from the Dunkirk, altho the removal of calcium was greater.

Effect of plant growth on removal of magnesium

The effect of plant growth on the removal of magnesium is brought out by table 20. It will be seen that there is a greater loss of magnesium in

TABLE 20. AVERAGE ANNUAL REMOVAL OF MAGNESIUM FROM PLANTED AND FROM UNPLANTED TANKS

(In pounds per acre)

Tanks	Soil treatment	Magnesium removed in		Total magnesium removed
		Drainage water	Crops	
13, 15	Planted	30.6	3.5	34.1
14, 16	Bare	45.4	.....	45.4
Magnesium conserved by cropping				11.3

the drainage water of the uncropped soil than in both the drainage and the crops of the planted soil. The large quantity of magnesium leached from the bare soil is apparently caused mainly by the solvent action of the nitric acid, as was the case with calcium.

Not only is the total removal of magnesium greater from the bare than from the planted soil, but its concentration is greater in the water from the uncropped soil, as may be seen from table 21:

TABLE 21. AVERAGE MAGNESIUM CONTENT OF DRAINAGE WATER FROM PLANTED AND FROM UNPLANTED TANKS

Tank	Soil treatment		Magnesium (parts per million)	
	Crop	Lime	For each tank	Average for crop treatment
13	Planted	Not limed	6.1	6.3
15	Planted	Limed	6.6	
14	Bare	Not limed	7.3	8.2
16	Bare	Limed	9.2	

Effect of liming on removal of magnesium

The effect of liming the soil was to increase the removal of magnesium both in the leachings and in the crops, as may be seen in table 22. There

TABLE 22. AVERAGE ANNUAL REMOVAL OF MAGNESIUM FROM LIMED AND FROM UNLIMED TANKS

(In pounds per acre)

Soil treatment	Tank	Magnesium removed from planted tanks			Tank	Magnesium leached from corresponding unplanted tanks
		In drainage water	In crops	Total		
Not limed	13	29.6	3.06	32.66	14	39.30
Limed	15	31.7	3.93	35.63	16	51.60

appears to be a basic exchange, similar to that which occurred in the Dunkirk soil, by which magnesium was liberated and dissolved by the soil water. The concentration of magnesium also was greater in the drainage water from the limed soil than in that from the unlimed, as may be seen in table 21.

REMOVAL OF POTASSIUM

Potassium differs from the other bases that were determined in the Dunkirk soil in that it was removed in greater quantities by the crops than by the drainage water. This was not true of the removal of potassium from the Volusia soil.

Effect of plant growth on removal of potassium

In spite of the fact that less potassium was removed by crops than by drainage water in these experiments, the total removal of potassium was greater from the planted than from the bare tanks. This is entirely contrary to the removal of calcium from the same tanks, as may be seen in table 23:

TABLE 23. AVERAGE ANNUAL REMOVAL OF POTASSIUM FROM PLANTED AND FROM UNPLANTED TANKS

(In pounds per acre)

Tanks	Soil treatment	Potassium removed in		Total potassium removed
		Drainage water	Crops	
13, 15	Planted	73.2	34.1	107.3
14, 16	Bare	84.5	.....	84.5
Potassium conserved by not cropping				22.8

While the growth of crops conserved the calcium in the soil, the same operation increased the loss of potassium. There was little difference in the concentration of potassium in the drainage water from the planted and from the bare tanks, as is shown in table 24:

TABLE 24. AVERAGE POTASSIUM CONTENT OF DRAINAGE WATER FROM PLANTED AND FROM UNPLANTED TANKS

Tank	Soil treatment		Potassium in drainage water (parts per million)	
	Crop	Lime	For each tank	Average for crop treatment
13	Planted	Not limed	18.3	15.9
15	Planted	Limed	13.6	
14	Bare	Not limed	15.5	14.0
16	Bare	Limed	12.5	

In respect to the concentration of potassium in the drainage water from the bare and from the planted tanks, the Volusia and the Dunkirk soils are in accord. It is probable that this is to be accounted for, in part at least, by the greater volume of percolate from the bare soil, but it seems possible that the plant growth effects a solvent action on the soil potassium which is indicated by the fact that the total removal of potassium in the crops and in the drainage combined is greater than that in the drainage from the bare soil.

Effect of liming on removal of potassium

The application of lime to this soil resulted in a decrease in the quantities of potassium contained in the drainage water and in the crops. This is shown in table 25:

TABLE 25. AVERAGE ANNUAL REMOVAL OF POTASSIUM FROM LIMED AND FROM UNLIMED TANKS

(In pounds per acre)

Soil treatment	Tank	Potassium removed from planted tanks			Tank	Potassium leached from corresponding unplanted tanks
		In drainage water	In crops	Total		
Not limed	13	88.6	35.08	123.68	14	99.1
Limed	15	57.8	33.12	90.92	16	69.9

There is nothing in this experiment to indicate that the application of lime caused the liberation of potassium. The same was true of the experiment with Dunkirk soil. It may be remarked, however, that if the application of lime did liberate any potassium from the surface soil, it may have been absorbed by the lower layers of soil and thus have been removed from the drainage water.

The concentration of the drainage water from the limed and from the unlimed soil does not give any more indication of the liberation of potassium than do the quantities removed. The concentration of potassium is stated in table 26:

TABLE 26. POTASSIUM CONTENT OF DRAINAGE WATER FROM LIMED AND FROM UNLIMED TANKS

Tank	Soil treatment		Potassium (parts per million)
	Crop	Lime	
13	Planted	Not limed	18.3
15	Planted	Limed	13.6
14	Bare	Not limed	15.5
16	Bare	Limed	12.5

REMOVAL OF SULFUR

Sulfur was recovered in the drainage water as sulfate, and it is significant that the years in which the content of sulfur in the drainage water was large were the years in which the removal of nitrogen by leaching was large. Drainage water from the Volusia soil contained somewhat less sulfur than did that from the Dunkirk, but the crops on the former soil contained as much sulfur as did those on the latter altho the yields were much smaller.

Effect of plant growth on removal of sulfur

There is one respect in which nitrogen and sulfur differ radically in this experiment, and that is in the proportion removed by crops and by drainage water, respectively. Nitrogen is removed most largely by the crops on planted soil, while sulfur is carried off mainly by the drainage water. The figures for sulfur in crops and in drainage water during the period of the experiment are given in table 27. The total quantity of

TABLE 27. SULFUR IN DRAINAGE WATER AND IN CROPS
(In pounds per acre, annual average)

Tank	Lime treatment	Sulfur in drainage water	Sulfur in crops	Total sulfur
13	Not limed	35.2	9.6	44.8
14	Not limed	43.3	.....	43.3
15	Limed	33.7	10.7	44.4
16	Limed	39.0	.....	39.0

sulfur removed from the planted tanks is not materially different from that removed from the bare tanks.

Effect of liming on removal of sulfur

In the experiments with Dunkirk soil the application of lime was accompanied by an increase in the quantity of sulfur in the drainage water. In the present experiments this was not the case, as may be seen in table 28:

TABLE 28. AVERAGE ANNUAL REMOVAL OF SULFUR FROM LIMED AND FROM UNLIMED TANKS

(In pounds per acre)

Soil treatment	Tank	Sulfur removed from planted tanks			Tank	Sulfur leached from corresponding unplanted tanks
		In drainage water	In crops	Total		
Not limed	13	35.2	9.6	44.8	14	43.3
Limed	15	33.7	10.7	44.4	16	39.0

Liming the Dunkirk soil did not result in an increased formation of nitrates but apparently favored sulfofication. Application of lime to the Volusia soil was accompanied by increased nitrification but had no effect on the production of sulfates. This would perhaps indicate that the conditions favorable to one of these fermentations are not always favorable to the other.

REMOVAL OF PHOSPHORUS

The Volusia soil, like the Dunkirk, has never furnished more than a trace of phosphorus in the drainage water. The data on removal of this element are therefore confined to the ash analyses of the crops. The average annual removal of phosphorus (calculated to the element P) is shown in table 29:

TABLE 29. PHOSPHORUS IN CROPS
(In pounds per acre, annual average)

Tank	Soil treatment	Phosphorus in crops
13	Not limed	9.36
15	Limed	11.12

There is a larger annual removal of phosphorus in the crops grown on the limed soil than in those from the unlimed soil. This was borne out by the data for each year, which are given in table 7 of the appendix (page 92). The year 1913 was the only one in which more phosphorus did not appear in the limed crops. In this respect there was no similarity between the Volusia and the Dunkirk soil, the latter having shown no increase in the quantity of phosphorus in the crops grown on the limed soil.

DIVERGENT EFFECTS OF LIMING THE TWO SOILS

Comparison of the results of applications of lime to the Dunkirk soil with those obtained from the Volusia soil shows some striking differences. It will be remembered that the Dunkirk soil contained about 50 per cent more calcium in the surface foot than does the Volusia soil, and that this ratio gradually increased with the depth, the fourth foot of the Dunkirk soil containing 319 per cent more than the corresponding layer of the Volusia. The lime requirement of the two soils by the Veitch method was about the same when averaged for the four feet, altho it was slightly greater in the surface foot of the Volusia. It is evident that the lime requirement as determined is not a measure of the calcium content of these soils.

In the light of this information it is interesting to observe the effect of liming in order to ascertain whether the calcium content or the lime requirement is the better guide to the need of the soils for lime as expressed by their response in crop yield. The records for the Dunkirk soil show that there was no larger yield on the limed tanks than on the unlimed. On the Volusia soil there was a consistently larger yield on the limed soil each

year except the first, and this increase averaged somewhat more than 12 per cent for the five-years period. The calcium content therefore appears to be a better guide to the need of these soils for lime than does the lime requirement as determined by the Veitch method. The data at hand are too limited to admit of generalization, but they may be worth further consideration.

Greater crop yield on the limed Volusia soil was accompanied by more nitrogen in the drainage water and also by more calcium. On the Dunkirk soil neither of these constituents was found in greater quantity in the drainage water from the limed tanks than from the unlimed. It may be remarked also that analyses of the soil air aspirated from the tanks, as reported in a previous publication,[4] showed no appreciable difference between the limed and the unlimed Dunkirk soil, but in the Volusia soil the carbon-dioxide content of the soil air was much increased by liming.

The fact that nitrate nitrogen in the drainage water and carbon dioxide in the soil air were present in larger amounts in the limed Volusia than in the unlimed gives evidence that decomposition of the organic matter proceeded more rapidly when lime was applied to that soil. This, however, was not the case with the Dunkirk soil, and there is presented the rather unlooked-for situation in which lime increased decomposition of organic matter in one soil but did not do so in the other soil.

A possible explanation for this divergent effect of lime on the two soils is suggested by the quantity of calcium in their respective drainage waters. As before stated, the application of lime had no effect on the removal of calcium in the drainage water from the Dunkirk soil, but it increased markedly the quantity of calcium removed from the Volusia soil. It seems probable that by increasing the concentration of calcium in the soil water, the ammonifying, nitrifying, and other bacteria concerned in decomposition of organic matter were afforded a more congenial environment. If liming did not increase the concentration of calcium in the soil water, as was the case with the Dunkirk soil, there was no acceleration of decomposition.

This experiment would seem to demonstrate one way in which liming may benefit soils. Certainly a larger amount of nitrate nitrogen was placed at the disposal of the plants, and the increased decomposition

[4] Bizzell, J. A., and Lyon, T. L. The effect of certain factors on the carbon-dioxide content of soil air. Amer. Soc. Agron. Journ. **10**: 97–112. 1918.

doubtless rendered other plant nutrients more available by breaking down the compounds in which they were held, as, for instance, the phosphorus of organic matter.

SUMMARY

The object of the experiments here described was to observe the removal, by drainage water and by crops, of calcium and certain other soil constituents from Volusia silt loam. This soil is a rather unproductive type widely distributed over the hills of southern New York. The experiments continued thru a period of five years.

The average annual rainfall for the five years was 32.97 inches. Of the annual rainfall, 27.13 inches, or 82.3 per cent, percolated thru the unplanted soil, and 20.62 inches, or 62.5 per cent, percolated thru the cropped soil. About two-fifths of the rainfall passed into the air from the surface of the soil and thru the plants growing on it.

Application of burnt lime had no appreciable effect on the proportion of rainfall that percolated thru the soil. Similar experiments with Dunkirk soil reported elsewhere gave similar results. Liming either of these soils would probably not facilitate the removal of water thru tile drains.

The average evapo-transpiration ratio for the cropped soils was 1:908, the crops being maize, field peas, oats two years, and barley. The average minimum transpiration ratio for the same crops was 1:451. Both of these ratios were much wider for the Volusia soil of these experiments than for the Dunkirk soil in the experiments previously reported. In this comparison the soil having the greater production of dry matter in crops per unit of water used was the one that had the greater concentration of total solids in the drainage water.

The application of lime apparently favored the production of nitrates in the Volusia soil used in these experiments, while it had no such effect on the Dunkirk soil. The lime requirement of the Dunkirk soil as determined by the Veitch method is very little less than that of the Volusia. The percentage of calcium is about one-third less in the surface foot of the Volusia. In this case the relative calcium content of the soil is a better guide to the need of the soil for lime than is the lime requirement as determined.

The amount of nitrogen in the maize, allowing for that in the roots, added to that in the drainage water from the same tanks, was greater than the amount in the drainage water from the corresponding bare tanks; while

in the case of oats the amount of nitrogen in the crop and in the drainage water was less than in the drainage water from bare soil. The same relation held with the Dunkirk soil.

The quantity of calcium in the drainage water of the unplanted soil was greater than that in the crops and the drainage water combined from the cropped soil. Therefore the process of cropping conserves the calcium in the soil even when the crops are removed. This may be accounted for, in part at least, by the large formation and leaching of nitrates from bare soil.

Apparently the application of burnt lime to the Volusia soil increased the amount of soluble calcium in that soil, but this was not the case with the Dunkirk soil. The Volusia soil has a greater lime requirement and a lower calcium content than has the Dunkirk soil.

To keep the soil supply of calcium up to its present amount would require an annual application of 536 pounds of pure burnt lime, or 957 pounds of pure limestone, to supply the bare soil, and 371 pounds of burnt lime, or 662 pounds of limestone, to supply the planted soil.

Magnesium was present in the drainage water in much smaller quantity than was calcium. Application of lime to the soil increased the quantity of magnesium in the drainage water. Cropping decreased the removal of magnesium from the soil. These relations were the same as for the Dunkirk soil.

Potassium was removed in larger quantity in the drainage water than in the crops, in which respect the Volusia soil differed from the Dunkirk soil. It agreed with the latter, however, in that the application of lime did not increase the quantity of potassium in the drainage water nor in the crops.

Cropping did not materially affect the total removal of sulfur from the soil. Applications of lime resulted in a slight decrease in the sulfur removed in the drainage water. With the Dunkirk soil, applications of lime increased the amount of sulfur removed in the drainage water.

Phosphorus was present in the drainage water only in amounts too small to be determined. Applications of lime increased the removal of phosphorus in the crops. With the Dunkirk soil, applications of lime did not increase the removal of phosphorus in the crops.

Memoir 38, *The Crane-Flies of New York. Part II. Biology and Phylogeny*, the third preceding number in this series of publications, was mailed on July 18, 1921.

Memoir 39, *The Genetic Relations of Plant Colors in Maize*, the second preceding number in this series of publications, was mailed on July 19, 1921.

APPENDIX

TABLE 1. Crop Yields from Lysimeter Tanks 13 and 15 during the Period from 1913 to 1917, Expressed as Dry Matter

Year	Tank	Crop	Per tank			Per acre		
			Grain (grams)	Cob (grams)	Straw, stover, or vines (grams)	Grain (bushels)	Cob (tons)	Straw, stover, or vines (tons)
1913	13	Oats	364.2	.....	302.3	62.4	.....	0.83
	15	Oats	337.5	.....	285.5	57.8	.....	0.78
1914	13	Peas	95.6	.....	452.2	8.8	.....	1.24
	15	Peas	172.9	.....	486.5	15.8	.....	1.34
1915	13	Maize	31.2	22.5	746.3	3.0	0.06	2.05
	15	Maize	121.6	68.4	821.8	11.9	0.18	2.26
1916	13	Oats	184.8	.....	266.7	31.6	.....	0.72
	15	Oats	181.0	.....	293.5	31.0	.....	0.80
1917	13	Barley	148.4	.....	161.2	17.0	.....	0.44
	15	Barley	191.0	.....	212.0	21.8	.....	0.58

TABLE 2. Flow of Drainage Water from Lysimeter Tanks 13 to 16 from May 1, 1913, to April 30, 1918

(In liters)

Year and month	Tank			
	13	14	15	16
1913–May	56.8	71.2	70.4	72.0
June	2.4	24.0	3.2	23.2
July	0.0	5.6	0.8	4.8
August	0.4	0.8	0.0	0.0
September	17.6	72.0	0.8	67.2
October	37.6	124.0	26.4	92.0
November	91.6	115.2	79.2	89.6
December	49.2	54.0	44.8	41.6
1914–January	87.6	90.8	116.0	156.4
February	27.2	51.2	38.0	40.4
March	159.2	211.6	206.8	188.0
April	220.8	288.4	215.2	149.2
Totals	750.4	1,108.8	801.6	924.4

TABLE 2 (*continued*)

Year and month	Tank			
	13	14	15	16
1914–May	102.4	130.0	98.4	100.0
June	24.8	59.2	22.4	65.6
July	0.0	23.2	0.4	16.8
August	5.6	220.0	0.0	152.0
September	17.6	64.0	3.2	87.2
October	0.0	2.4	0.0	0.0
November	0.4	19.2	0.0	4.0
December	28.4	55.2	15.6	57.2
1915–January	221.6	278.0	246.8	285.2
February	224.0	179.2	339.6	304.0
March	5.2	2.4	12.0	3.2
April	5.6	1.6	3.2	1.6
Totals	635.6	1,034.4	741.6	1,076.8
1915–May	18.0	25.2	14.4	31.2
June	77.2	85.6	63.2	66.8
July	242.0	292.0	183.6	234.0
August	26.8	114.8	10.0	94.4
September	14.4	75.6	6.0	52.8
October	146.8	178.0	111.2	144.4
November	29.2	43.6	26.4	30.8
December	69.2	67.2	56.0	66.4
1916–January	90.4	86.4	72.8	73.6
February	4.8	8.0	6.4	5.2
March	96.8	143.6	109.6	137.6
April	238.8	268.4	187.6	178.4
Totals	1,054.4	1,388.4	847.2	1,115.6
1916–May to June 5	166.0	165.6	100.4	114.8
June 6				
July				
August	241.6	454.8	224.0	366.0
September				
October				
November				
December	76.8	72.8	85.2	65.6
1917–January 15				
January 16				
February				
March	162.4	142.8	130.0	132.8
April				
Totals	646.8	836.0	539.6	679.2

TABLE 2 (*concluded*)

Year and month	Tank			
	13	14	15	16
1917–May	178.8	194.8	171.6	172.4
June	282.0	345.6	228.0	330.0
July	46.8	80.8	39.6	83.2
August	268.4	296.4	214.0	318.4
September	48.8	62.4	57.6	61.6
October	203.2	219.6	186.0	216.0
November	24.0	20.0	22.4	17.2
December	15.2	17.6	24.8	24.8
1918–January	0.4	0.0	1.2	0.0
February	0.0	64.4	50.8	52.8
March	32.0	73.6	29.2	66.8
April	192.8	143.2	152.8	142.8
Totals	1,292.4	1,518.4	1,178.0	1,486.0
Grand totals	4,379.6	5,886.0	4,108.0	5,282.0

TABLE 3. FLOW OF DRAINAGE WATER FROM LYSIMETER TANKS 13 TO 16 FROM MAY 1, 1913, TO APRIL 30, 1918

(In acre inches)

Period	Tank			
	13	14	15	16
May 1, 1913, to April 30, 1914	18.23	26.94	19.48	22.46
May 1, 1914, to April 30, 1915	15.44	25.13	18.02	26.17
May 1, 1915, to April 30, 1916	25.62	33.74	20.59	27.11
May 1, 1916, to April 30, 1917	15.72	20.31	13.11	16.50
May 1, 1917, to April 30, 1918	31.40	36.90	28.62	36.11
Average annual percolation	21.28	28.60	19.96	25.67

TABLE 4. METEOROLOGICAL RECORDS AT ITHACA, MAY 1, 1913, TO APRIL 30, 1918
Data by months

Year and month	Rainfall (inches)	Temperature (degrees Fahrenheit)			Hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m. (per cent)
		Mean maximum	Mean minimum	Mean			
1913–May	3.15	66.2	44.5	55.4	286.9	9.8	73
June	2.00	78.6	51.4	65.0	332.2	7.5	68
July	1.59	82.5	68.2	70.4	304.7	8.4	69
August	1.92	82.0	57.2	69.6	304.2	8.2	71
September	3.28	73.0	49.2	61.1	219.7	8.1	76
October	3.63	61.3	45.4	53.4	152.5	9.4	86
November	2.21	51.5	35.8	43.6	101.5	11.9	81
December	1.94	39.8	25.3	32.6	84.9	10.0	83
1914–January	1.37	33.7	19.3	26.5	55.7	13.8	85
February	1.62	27.0	8.5	17.8	151.4	11.6	82
March	1.90	39.1	24.3	31.7	141.7	10.3	82
April	4.35	51.1	33.1	42.1	144.8	11.6	78
May	3.63	71.1	47.5	59.3	297.7	8.1	71
June	4.75	76.5	54.5	65.5	301.2	8.5	74
July	1.89	81.2	59.2	70.2	230.8	7.0	78
August	6.10	80.2	58.2	69.2	208.4	7.0	80
September	1.96	71.1	48.2	59.6	255.2	7.6	82
October	1.38	63.6	43.9	53.8	212.5	8.7	86
November	0.68	46.4	31.1	38.8	111 9	12.5	78
December	2.70	32.9	19.1	26.0	73.3	10.4	82
1915–January	5.02	33.4	19.7	26.6	96.0	10.4	85
February	1.83	37.8	22.7	30.2	94.1	11.9	86
March	0.32	37.5	21.9	29.7	183.5	10.9	83
April	0.55	62.7	39.6	51.2	202.2	9.0	70
May	2.44	61 6	41.6	51.6	187.7	8.4	74
June	3.94	75.7	51.6	63.6	273.4	8.4	69
July	6.18	80.2	58.2	69.2	212.8	6.3	82
August	3.70	75.0	57.5	66.2	174.0	7.9	86
September	2.58	75.6	54.1	64.8	203.6	7.9	86
October	4.10	59.9	43.7	51.8	155.8	9.4	83
November	1.10	47.7	33.1	40.4	107.9	12.1	73
December	2.90	33.6	23.3	28.4	42.6	12.0	84
1916–January	0.81	40.0	23.7	31.8	73.7	12.2	80
February	2.97	30.1	13.0	21.6	87.8	10.1	83
March	2.28	35.3	18.7	27.0	162.5	10.9	81
April	2.77	53.7	37.0	45.4	133.4	8.4	80
May	4.27	68.4	46.9	57.6	189.2	10.6	71
June	3.48	70.9	51.9	61.4	171.0	9.8	79
July	1.29	85.8	63.5	74.6	226.7	7.8	77
August	1.50	83.7	58.7	71.2	283.2	7.3	75
September	5.65	72.8	50.9	61.8	232.7	9.5	73
October	1.59	63.1	39.6	51.4	180.5	9.7	74
November	1.53	46.7	31.4	39.0	88.5	10.2	77
December	1.01	35.9	22.0	29.0	99.9	12.1	79

TABLE 4 (*continued*)

Year and month	Rainfall (inches)	Temperature (degrees Fahrenheit)			Hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m. (per cent)
		Mean maximum	Mean minimum	Mean			
1917–January	1.82	34.1	17.7	25.9	101.8	12.9	84
February	0.70	29.6	10.4	20.0	99.1	13.5	86
March	1.59	41.9	25.9	33.9	127.1	14.2	78
April	1.83	52.4	35.5	44.0	140.9	10.9	75
May	4.41	56.7	40.0	48.4	107.9	10.6	72
June	7.35	74.1	53.6	63.8	167.8	8.0	76
July	3.25	81.4	61.6	71.5	250.8	7.5	76
August	8.45	79.9	58.5	69.2	244.8	7.5	80
September	2.22	69.9	47.2	58.6	231.2	7.6	82
October	4.84	53.6	36.7	45.2	77.8	10.8	81
November	0.64	43.3	26.4	34.8	93.6	9.6	81
December	2.48	26.9	10.7	18.8	72.2	12.1	82
1918–January	1.83	22.0	6.8	14.4	127.0	10.9	79
February	1.48	35.0	13.7	24.4	104.8	14.6	77
March	2.58	48.2	25.3	36.8	178.6	11.3	73
April	3.54	56.3	35.2	45.8	171.2	10.3	75

Average of each month

Month	Rainfall (inches)	Temperature (degrees Fahrenheit)			Hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m. (per cent)
		Mean maximum	Mean minimum	Mean			
May	3.58	64.8	44.1	54.5	213.9	9.5	72.2
June	4.30	75.2	52.6	63.9	249.1	8.4	73.2
July	2.84	82.2	62.1	71.2	245.2	7.4	76.4
August	4.33	80.2	58.0	69.1	242.9	7.6	78.4
September	3.14	72.5	49.9	61.2	228.5	8.1	79.8
October	3.11	60.3	41.9	51.1	155.8	9.6	82.0
November	1.23	47.1	31.6	39.3	100.7	11.3	79.0
December	2.21	33.8	20.1	26.96	74.6	11.3	82.0
January	2.17	32.6	17.4	25.0	91.0	12.0	82.6
February	1.72	31.9	13.7	22.8	107.4	12.3	82.8
March	1.73	40.4	23.2	31.8	158.7	11.5	79.4
April	2.60	55.2	36.1	45.7	158.5	10.0	75.6

TABLE 4 (*concluded*)
Data by years

Year	Total rainfall (inches)	Temperature (degrees Fahrenheit)			Total hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m. (per cent)
		Mean maximum	Mean minimum	Mean			
May 1913, to April 1914	28.96	57.2	38.5	47.4	2,281.2	10.1	77.8
May 1914, to April 1915	30.81	57.9	38.8	48.3	2,266.8	9.3	79.6
May 1915, to April 1916	35.77	55.7	37.9	46.8	1,815.2	9.5	80.5
May 1916, to April 1917	26.26	57.1	37.9	47.5	1,940.6	10.7	77.3
May 1917, to April 1918	43.07	53.9	34.6	44.3	1,827.7	10.1	77.8

TABLE 5. SUBSTANCES CONTAINED IN DRAINAGE WATER, IN PARTS PER MILLION

	Tank			
	13	14	15	16
1913–14	TOTAL SOLIDS			
May 1–September 30	246	314	237	422
October 1–April 30	177	220	199	310
1914–15				
May 1–September 30	241	245	223	370
October 1–April 30	200	179	184	252
1915–16				
May 1–September 30	302	271	309	363
October 1–April 30	260	228	263	292
1916–17				
May 1–April 30	296	270	325	353
1917–18				
May 1–April 30	285	369	295	306
Averages	251	262	254	333.5
1913–14	NITRATES			
May 1–September 30	40.0	66.0	42.0	116.0
October 1–April 30	8.7	50.8	19.2	68.3
1914–15				
May 1–September 30	6.0	30.7	14.6	55.4
October 1–April 30	7.6	22.9	22.2	42.2
1915–16				
May 1–September 30	20.6	42.0	25.3	57.3
October 1–April 30	8.0	18.5	7.8	27 3
1916–17				
May 1–April 30	6.5	36.0	5.8	60.0
1917–18				
May 1–April 30	3.0	20.5	3.0	25.0
Averages	12.56	35.93	17.48	56.44

TABLE 5 (*continued*)

	Tank			
	13	14	15	16
	BICARBONATES			
1913–14				
May 1–September 30	170	197	169	213
October 1–April 30	142.3	126.8	153.8	146.8
1914–15				
May 1–September 30	170	163	168.75	207
October 1–April 30	161.1	131.5	127.3	135
1915–16				
May 1–September 30	200	171.5	226.5	251
October 1–April 30	212.5	153	201.5	206.5
1916–17				
May 1–April 30	244.3	194.5	288.8	246.8
1917–18				
May 1–April 30	255	217	280	234
Averages	194.4	169.29	201.96	205.01
	SULFATES			
1913–14				
May 1–September 30	23	33	39	57
October 1–April 30	22.8	15.9	18.3	15.5
1914–15				
May 1–September 30	10.6	7.1	13.9	8 0
October 1–April 30	17.2	23.4	12.2	14.3
1915–16				
May 1–September 30	36.0	22.6	22.4	22.9
October 1–April 30	34.8	26.3	33.0	23 0
1916–17				
May 1–April 30	34.5	27.0	34.5	27.0
1917–18				
May 1–April 30	21.5	16.3	19.4	19.2
Averages	25.05	21.46	24 09	23.36
	SILICA			
1913–14				
May 1–September 30	5.6	6.3	5.8	6.8
October 1–April 30	7.1	5.9	8.4	8.9
1914–15				
May 1–September 30	6.6	9.4	5.4	12.0
October 1–April 30	6.6	4.5	5.5	5.4
1915–16				
May 1–September 30	8.9	8.0	8.6	10.5
October 1–April 30	5.5	4.9	7.6	5.5
1916–17				
May 1–April 30	9.0	8.7	10.3	7.6
1917–18				
May 1–April 30	11.8	11.4	10.3	10.2
Averages	7.64	7.39	7.74	8.36

TABLE 5 (*continued*)

	Tank			
	13	14	15	16
	PHOSPHATES			
1913–14				
May 1–September 30	None	None	None	None
October 1–April 30	.....	.....	.....	.....
1914–15				
May 1–September 30	Trace	Trace	None	Trace
October 1–April 30	Trace	Trace	Trace	Trace
1915–16				
May 1–September 30	None	None	None	None
October 1–April 30	None	None	None	None
1916–17				
May 1–April 30	Trace	Trace	Trace	Trace
1917–18				
May 1–April 30	None	None	None	None
	CALCIUM			
1913–14				
May 1–September 30	38.5	56.3	40.9	70.8
October 1–April 30	42.2	49.8	49.7	62.4
1914–15				
May 1–September 30	46.1	49.0	47.5	77.2
October 1–April 30	65.3	37.8	43.8	52.8
1915–16				
May 1–September 30	52.8	50.8	64.7	71.0
October 1–April 30	49.3	41.0	50.1	62.1
1916–17				
May 1–April 30	58.1	52.9	71.7	77.5
1917–18				
May 1–April 30	56.6	54.2	63.1	64.4
Averages	51.12	48.99	53.95	67.28
	MAGNESIUM			
1913–14				
May 1–September 30	5.8	7.6	6.8	9.0
October 1–April 30	6.3	6.7	6.9	9.4
1914–15				
May 1–September 30	5.6	6.0	6.0	9.2
October 1–April 30	4.5	4.2	3.6	5.4
1915–16				
May 1–September 30	7.8	7.6	7.9	3.6
October 1–April 30	6.7	5.1	8.3	8.1
1916–17				
May 1–April 30	6.6	8.5	9.6	11.0
1917–18				
May 1–April 30	5.8	6.1	7.1	7.9
Averages	6.15	6.48	7.04	9.22

TABLE 5 (*concluded*)

	Tank			
	13	14	15	16
	POTASSIUM			
1913–14				
May 1–September 30	12.4	9.5	11.3	13.8
October 1–April 30	8.3	8.3	6.1	7.1
1914–15				
May 1–September 30	16.1	16.9	11.5	12.2
October 1–April 30	8.9	8.6	5.0	6.0
1915–16				
May 1–September 30	29.7	21.6	20.7	17.2
October 1–April 30	18.9	13.8	14.3	9.9
1916–17				
May 1–April 30	22.6	18.7	17.4	14.4
1917–18				
May 1–April 30	22.2	18.6	16.7	15.1
Averages	17.40	14.51	12.87	11.96
	SODIUM			
1913–14				
May 1–September 30	15.6	12.9	11.3	10.2
October 1–April 30	22.9	22.5	24.0	22.6
1914–15				
May 1–September 30	17.5	13.9	12.7	16.7
October 1–April 30	22.9	17.9	17.8	15.2
1915–16				
May 1–September 30	24.5	19.8	19.9	20.7
October 1–April 30	26.0	18.9	24.9	18.9
1916–17				
May 1–April 30	18.4	13.7	18.5	13.6
1917–18				
May 1–April 30	18.7	14.4	16.9	13.7
Averages	20.83	16.77	18.25	16.45
	CARBONATES			
1913–14				
May 1–September 30	None	None	None	None
October 1–April 30	None	None	None	None
1914–15				
May 1–September 30	3.68	Trace	Trace	4.92
October 1–April 30	None	None	None	None
1915–16				
May 1–September 30	7.62	6.40	None	7.37
October 1–April 30	7.84	4.41	9.31	4.90
1916–17				
May 1–April 30	None	None	None	None
1917–18				
May 1–April 30	None	None	None	None
Averages	2.39	1.35	1.16	2.15

TABLE 6. SUBSTANCES CONTAINED IN DRAINAGE WATER, IN POUNDS PER ACRE

	Tank			
	13	14	15	16
	TOTAL SOLIDS			
1913–14				
May 1–September 30	104.1	299.2	97.6	387.9
October 1–April 30	656.7	1,133.9	796 7	1,293.7
Totals	760.8	1,433.1	894.3	1,681.6
1914–15				
May 1–September 30	198.9	669.4	152.0	857.9
October 1–April 30	534.4	530.6	625.4	909.1
Totals	733.3	1,200.0	777.4	1,767.0
1915–16				
May 1–September 30	629.6	835.7	471.9	958.4
October 1–April 30	968.4	999.0	826.0	1,023.9
Totals	1,598.0	1,884.7	1,297.9	1,982.3
1916–17				
May 1–April 30	1,054.9	1,243.7	966.2	1,322.6
1917–18				
May 1–April 30	2,028.0	1,986.5	1,914.6	2,505.3
Yearly averages	1,235.0	1,549.6	1,170.1	1,851.7
	NITRATES			
1913–14				
May 1–September 30	16.5	62.8	17.1	106.3
October 1–April 30	32.4	261.8	76.8	285.1
Totals	48.9	324.6	93.9	391.4
1914–15				
May 1–September 30	4.9	83.7	9.9	128.4
October 1–April 30	20.4	67.7	75.5	90.9
Totals	25.3	151.4	85.4	219.3
1915–16				
May 1–September 30	42.9	137.2	38.6	151.2
October 1–April 30	29.8	81.0	24.5	95.7
Totals	72.7	218.2	63.1	246.9
1916–17				
May 1–April 30	23.1	165.8	17.2	224.8
1917–18				
May 1–April 30	20.9	171.3	19.3	204.4
Yearly averages	38.2	206.2	55.8	257.3

TABLE 6 (*continued*)

	Tank			
	13	14	15	16
	BICARBONATES			
1913–14				
May 1–September 30	71.6	187.3	69.4	195.6
October 1–April 30	527.9	653.5	615.7	612.6
Totals	599.5	840.8	685.1	808.2
1914–15				
May 1–September 30	140.5	445.2	115.1	479.9
October 1–April 30	430.3	389.5	432.5	487.1
Totals	570.8	834.7	547.6	967.0
1915–16				
May 1–September 30	417.0	560.5	345.9	662.7
October 1–April 30	791.5	670.3	632.8	724.1
Totals	1,208.5	1,230.8	978.7	1,386.8
1916–17				
May 1–April 30	870.6	895.9	858.6	924.7
1917–18				
May 1–April 30	1,814.9	1,814.9	1,817.2	1,915.9
Yearly averages	1,012.8	1,123.4	977.4	1,200.5
	SULFATES			
1913–14				
May 1–September 30	9.3	31.4	15.9	52.3
October 1–April 30	84.6	81.9	73.2	64.7
Totals	93.9	113.3	89.1	117.0
1914–15				
May 1–September 30	8.8	19.2	9.3	18.1
October 1–April 30	45.7	68.8	41.3	51.2
Totals	54.5	88.0	50.6	69.3
1915–16				
May 1–September 30	75.0	73.8	34.2	60.4
October 1–April 30	129.6	115.2	103.6	80.6
Totals	204.6	189.0	137.8	141.0
1916–17				
May 1–April 30	122.9	123.3	102.5	101.1
1917–18				
May 1–April 30	152.6	136.1	125.6	157.0
Yearly averages	125.7	129.9	101.1	117.1

TABLE 6 (*continued*)

	Tank			
	13	14	15	16
	SILICA			
1913–14				
May 1–September 30	2.2	6.0	2.2	6.0
October 1–April 30	26.3	30.4	33.6	37.1
Totals	28.5	36.4	35.8	43.1
1914–15				
May 1–September 30	5.5	25.3	3.3	27.5
October 1–April 30	17.6	13.2	18.7	19.3
Totals	23.1	38.5	22.0	46.8
1915–16				
May 1–September 30	18.5	26.1	13.1	27.7
October 1–April 30	20.5	21.4	23.8	19.3
Totals	39.0	47.5	36.9	47.0
1916–17				
May 1–April 30	32.0	40.3	31.8	24.4
1917–18				
May 1–April 30	83.7	95.3	66.6	83.2
Yearly averages	41.2	51.6	38.6	48.9
	CALCIUM			
1913–14				
May 1–September 30	15.9	53.4	16.5	65.0
October 1–April 30	156.4	256.8	198.9	260.4
Totals	172.3	310.2	215.4	325.4
1914–15				
May 1–September 30	38.0	133.9	32.5	179.0
October 1–April 30	174.1	111.8	148.7	190.6
Totals	212.1	245.7	181.2	369.6
1915–16				
May 1–September 30	110.0	165.0	98.9	187.6
October 1–April 30	183.8	179.8	157.5	217.7
Totals	293.8	344.8	256.4	405.3
1916–17				
May 1–April 30	207.0	243.6	213.1	290.3
1917–18				
May 1–April 30	402.8	452.9	409.4	526.7
Yearly averages	257.6	319.4	255.1	383.4

TABLE 6 (*continued*)

	Tank			
	13	14	15	16
	MAGNESIUM			
1913–14				
May 1–September 30	2.2	7.1	2.7	8.2
October 1–April 30	23.4	34.5	27.6	39.4
Totals	25.6	41.6	30.3	47.6
1914–15				
May 1–September 30	4.4	15.9	3.8	20.9
October 1–April 30	12.1	12.1	12.1	19.3
Totals	16.5	28.0	15.9	40.2
1915–16				
May 1–September 30	16.3	25.0	12.1	36.0
October 1–April 30	24.9	22.3	26.0	28.5
Totals	41.2	47.3	38.1	64.5
1916–17				
May 1–April 30	23.5	39.1	28.5	41.2
1917–18				
May 1–April 30	41.3	50.7	45.7	64.4
Yearly averages	29.6	41.3	31.7	51.6
	POTASSIUM			
1913–14				
May 1–September 30	4.9	8.8	4.4	12.6
October 1–April 30	30.9	42.8	24.2	29.8
Totals	35.8	51.6	28.6	42.4
1914–15				
May 1–September 30	13.2	46.3	7.7	28.1
October 1–April 30	23.1	25.3	16.5	21.5
Totals	36.3	71.6	24.2	49.6
1915–16				
May 1–September 30	61.9	70.7	31.6	45.4
October 1–April 30	70.5	60.4	44.9	34.7
Totals	132.4	131.1	76.5	80.1
1916–17				
May 1–April 30	80.5	86.1	51.7	53.9
1917–18				
May 1–April 30	158.1	155.4	108.0	123.4
Yearly averages	88.6	99.1	57.8	69.9

TABLE 6 (*concluded*)

	Tank			
	13	14	15	16
1913–14	SODIUM			
May 1–September 30	6.6	12.1	4.4	9.3
October 1–April 30	85.1	116.1	95.9	94.4
Totals	91.7	128.2	100.3	103.7
1914–15				
May 1–September 30	14.3	38.0	8.2	15.4
October 1–April 30	61.1	52.9	60.6	54.5
Totals	75.4	90.9	68.8	69.9
1915–16				
May 1–September 30	51.2	64.8	30.4	46.6
October 1–April 30	96.8	83.0	78.2	66.2
Totals	148.0	147.8	108.6	112.8
1916–17				
May 1–April 30	65.5	63.1	55.0	50.9
1917–18				
May 1–April 30	132.8	120.1	109.6	111.8
Yearly averages	102.7	110.0	88.4	89.8

TABLE 7. ASH AND ASH CONSTITUENTS IN CROPS, BY YEARS
(In percentage of dry matter)

Year	Tank	Crop	Part of crop	Ash	Ca	Mg	K	S	P
1913	13	Oats	Grain	3.67	0.03	0.06	0.62	0.24	0.56
	13	Oats	Straw	6.92	0.43	0.12	2.40	0.18	0.12
	15	Oats	Grain	3.39	0.04	0.03	0.62	0.23	0.56
	15	Oats	Straw	6.61	0.42	0.17	2.16	0.23	0.11
1914	13	Peas	Grain	4.30	0.05	0.04	1.15	0.36	0.48
	13	Peas	Straw	27.43	0.67	0.23	0.46	0.62	0.33
	15	Peas	Grain	3.43	0.04	0.04	1.14	0.33	0.48
	15	Peas	Straw	14.20	0.99	0.18	0.04	0.60	0.35
1915	13	Maize	Grain	1.74	0.03	0.09	0.38	0.30	0.36
	13	Maize	Straw	6.54	0.15	0.08	1.19	0.30	0.22
	15	Maize	Grain	1.60	0.06	0.07	0.42	0.18	0.37
	15	Maize	Straw	5.19	0.13	0.11	0.83	0.31	0.22
1916	13	Oats	Grain	3.33	0.02	0.03	0.77	0.19	0.47
	13	Oats	Straw	8.16	0.28	0.12	2.49	0.30	0.19
	15	Oats	Grain	3.88	0.01	0.04	0.67	0.18	0.52
	15	Oats	Straw	7.89	0.32	0.20	2.19	0.30	0.24
1917	13	Barley	Grain	3.01	0.03	0 02	0.54	0.21	0.52
	13	Barley	Straw	7.41	0.24	0.07	1.03	0.24	0.20
	15	Barley	Grain	2.92	0.02	0.03	0.58	0.20	0.50
	15	Barley	Straw	6.13	0.33	0.04	0.93	0.24	0.24

TABLE 8. ASH AND ASH CONSTITUENTS IN CROPS, BY YEARS
(In pounds per acre)

Year	Tank	Crop	Part of crop	Ash	Ca	Mg	K	S	P
1913	13	Oats	Grain	70.8	0.5	1.1	11.9	4.6	10.9
	13	Oats	Straw	116.9	7.3	2.0	40.5	3.1	2.0
	13	Oats	Total	187.7	7.8	3.1	52.4	7.7	12.9
	15	Oats	Grain	62.7	0.8	0.6	11.3	4.2	10.3
	15	Oats	Straw	103.2	6.1	2.6	33.7	3.5	1.7
	15	Oats	Total	165.9	6.9	3.2	45.0	7.7	12.0
1914	13	Peas	Grain	21.5	0.3	0.2	5.8	1.9	2.4
	13	Peas	Straw	679.5	16.5	5.7	11.3	5.5	8.2
	13	Peas	Total	701.0	16.8	5.9	17.1	17.4	10.6
	15	Peas	Grain	31.6	0.4	0.4	10.4	3.0	4.4
	15	Peas	Straw	391.2	27.4	4.9	11.4	16.6	9.6
	15	Peas	Total	422.8	27.8	5.3	21.8	19.6	14.0
1915	13	Maize	Grain	2.9	0.1	0.2	0.7	0.6	0.6
	13	Maize	Straw	264.8	6.0	3.2	47.9	12.0	9.0
	13	Maize	Total	267.7	6.1	3.4	48.6	12.6	9.6
	15	Maize	Grain	10.6	0.5	0.4	2.8	1.2	2.5
	5	Maize	Straw	231.7	5.7	4.9	37.2	13.6	9.9
	15	Maize	Total	242.3	6.2	5.3	40.0	14.8	12.4
1916	13	Oats	Grain	33.7	0.2	0.3	7.8	2.0	4.8
	13	Oats	Straw	118.1	4.1	1.8	36.1	4.3	2.8
	13	Oats	Total	151.8	4.3	2.1	43.9	6.3	7.6
	15	Oats	Grain	38.5	0.1	0.4	6.7	1.8	5.2
	15	Oats	Straw	126.1	5.3	3.3	35.1	4.8	3.8
	15	Oats	Total	164.6	5.4	3.7	41.8	6.6	9.0
1917	13	Barley	Grain	24.7	0.2	0.2	4.4	1.8	4.3
	13	Barley	Straw	65.6	2.2	0.7	9.1	2.1	1.8
	13	Barley	Total	90.3	2.4	0.9	13.5	3.9	6.1
	15	Barley	Grain	30.7	0.2	0.3	6.1	2.1	5.3
	15	Barley	Straw	72.9	3.9	1.7	11.0	2.9	2.9
	15	Barley	Total	103.6	4.1	2.0	17.1	5.0	8.2

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AGRICULTURAL EXPERIMENT STATION

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G. C. Supplee[1], W. A. Whiting, and P. A. Downs

The increasing importance of the liquid-milk supply for large centers of population and the greater demand for a better quality of raw material for manufacturing purposes have necessitated further knowledge of the methods used in determining the quality of milk, and particularly have emphasized the significance of bacteriological analyses.

Examination of milk for the purpose of determining numbers or types of bacteria seems to constitute the highest ideal in milk grading. This aspect is doubtless important and the respect for this method of procedure in judging milk quality should not be endangered. Obviously, the sanitary aspects of the milk problem must involve determinations of this kind. The significance of bacteria in the economic phases of the milk supply also becomes quite clear when it is remembered that the entire business of supplying milk to the urban population is founded on modern dairy science, of which the aims are maximum wholesomeness and maximum keeping quality. These two considerations have been responsible for the stress laid on the importance of bacteria counts in the milk industry at the present time.

That the methods of enumerating bacteria in milk have many shortcomings is well recognized by dairy bacteriologists. Bacteria counts, as now obtained, can be interpreted only on a comparative basis, and in no sense do they indicate the mathematical accuracy which their expression in numbers implies. Such comparative interpretations can be used only as indications of degrees of success in handling and of the variations of keeping quality. Undeniably this information is valuable in safeguarding the interests of consumers of milk in large cities, and its importance is shown by the report of the Committee on Statistics of Milk and Cream Regulations of the Official Dairy Instructors' Association (1917).[2] This committee obtained the complete milk regulations from 409 cities and

[1]At present Director of Research Department of the Dry Milk Company, New York.
[2]Dates in parentheses refer to *Literature Cited*, page 247.

towns in the United States, and found that 189 of these provided for a legal limit for bacteria in milk sold within the municipality. The limits allowed by these cities ranged from 50,000 to 5,000,000 to the cubic centimeter, with approximately one-half of the cities permitting a limit of 500,000. The necessity of fixing legal limits for bacteria in cream seems to have been regarded as much less important, since only 30 of the 409 cities had established legal limits for this product. The bacteria allowed in the latter case varied from 50,000 to 1,000,000 to the cubic centimeter.

These municipal regulations must of necessity imply provisions for their enforcement and for penalties for failures in their observance. Such provisions immediately bring into prominence the difficulty of application and enforcement of numerical bacterial standards. Unfortunately, the inherent inaccuracies of present methods of enumerating bacteria are too great to permit their results to be relied upon with the certainty of exactness which their fixed numerical standards would seem to warrant.

REVIEW OF PREVIOUS INVESTIGATIONS

The American Public Health Association (1915), recognizing the wide variations obtained by the ordinary, plating technique, have formulated, through their Laboratory Section, the following uniform method for determining bacteria in milk. This procedure, known as the "Standard Methods of Bacterial Analyses of Milk," has been of considerable value in securing uniform technique in different laboratories, and the results are comparable, since a uniform interpretation can be given to them. That the purpose of the Standard Methods is for securing uniform results rather than accurate counts, in the minimum length of time, is evident from the fact that 37° C. for forty-eight hours on plain agar is the only incubation temperature and medium recognized. In the routine examination of milk samples, the short incubation period has certain distinct advantages.

Conn (1915) compiled the results obtained from an exhaustive series of comparative determinations made from the same milk by four laboratories. This work, involving many thousand platings made under uniform procedure, nevertheless failed to give uniform and consistent results under those particular conditions. Viewed from the standpoint of absolutely accurate determinations of all bacteria present, there are numerous

reasons why the plate method gives widely discrepant results. Among the most important causes are: (1) the failure of certain species to produce visible colonies on the medium and in the incubation temperature used; (2) the tendency of many species to exist in groups of two or more individuals, which groups are broken apart with varying degrees of completeness during the plating operation; (3) too few or too many colonies to the plate; (4) the inhibiting or beneficial effect of diffused by-products from the growth of certain species on other species within the radius of diffusion; (5) the personal element involved in carrying out the method. Widely varying results from the same sample of milk under the same conditions of incubation temperature and medium would still be caused by the clumping tendency, by the number of colonies on each plate, and by the personal element entering into the manipulations.

Hill and Ellms (1897) early called attention to the unreliable results obtained from over-crowded plates used in water analysis. The Standard Methods stipulate that there shall be not less than 30, and not more than 200, colonies to the plate, altho Breed and Dotterrer (1916) conclude that limits of 30 and 400 are nearly as satisfactory.

Altho the Standard Methods call for plain agar incubated at 37° C. for forty-eight hours, comparative counts published from time to time have shown that a carbohydrate medium and a longer incubation period at a lower temperature have many advantages. Heinemann and Glenn (1908), from their work on the effect of incubation temperatures and media, reached the following conclusions:

1. Since pathogenic bacteria are always difficult, and in most cases impossible, to find in milk, a high temperature of incubation has no advantage over room temperature from this viewpoint.

2. Incubation at 20° C. is superior to incubation at 37° C. because both a higher count and a better differential count are obtained.

3. Dextrose is preferable to lactose as an addition to the medium.

4. Milk is usually consumed before the results of bacterial examinations are available. Accordingly bacteriological and chemical examinations should have as their principal objects the improvement and control of the general supply; and accuracy being of greater importance than quick results, the loss of a day in its interest is irrelevant.

Sherman (1916) points out the higher counts obtainable by the use of lactose agar in place of plain agar, and also the increase in the size of the colonies and the better differentiation of the types.

Breed and Stocking (1917) published a preliminary report on a series of comparative determinations, in which they conclude that the plate method, when used by careful workers, will give more reliable results than those reported by Conn, which had been obtained under routine conditions and possibly, in some instances, by inexperienced operators. Obviously, inexperience and carelessness are factors to be avoided in any method of enumerating bacteria, especially when the results are for the determination of municipal regulations. The same authors (1920), reporting a similar but more extensive investigation, found the plate method and the microscopic method (Breed method) productive of reasonably uniform and accurate results for the total number of bacteria present, all factors known to introduce inaccuracies having been first reduced to a minimum. For the plate method they report an average coefficient of variability of 8.3; for the microscopic determination of groups of bacteria, consisting of one or more individuals, 11.7; and for the microscopic determination of individual bacteria, 13.4. Altho these results are remarkably uniform, it must be remembered that they are obtained from samples which were artificially inoculated in order to reduce the clumping tendency to a minimum, and that the time and labor necessary to obtain this degree of accuracy by the microscopic method could not be expected in regular, routine examinations.

PRESENT EXPERIMENTS

Comparison of media and incubation temperatures

The experimental work reported herein was for the purpose of demonstrating the variations in counts obtained by plain and carbohydrate media at different incubation temperatures. It may indicate a further reason why the count at 37° C. for forty-eight hours, as used in routine work, may be more subject to discrepancies than counts obtained from longer incubation periods at lower temperatures.

The samples used for this work were selected at random from the ordinary market milk of the Ithaca city supply, at intervals extending over a period of one and one-half years. Twenty-seven plates were made from the same dilution of each sample. Nine of the plates were

poured with standard plain agar; nine with nutrient agar containing 1 per cent of dextrose; and nine with nutrient agar containing 1 per cent of lactose. The different agars were all made from single, large-quantity batches of plain, nutrient agar. These were subdivided, and the definite percentage of the particular carbohydrate desired was added to each. Three of the nine plates containing the different agars were incubated at 37° C. for forty-eight hours; three at 30° C. for five days; and three at 20° C. for five days. With the exceptions noted, the technique given in the Standard Methods was carefully followed. It was necessary, however, to include counts from plates containing fewer than 30 colonies and more than 200 colonies, altho in all cases the dilution was designed to give colonies between these limits from the forty-eight hour count at 37°.

In table 1 are shown the counts obtained from 100 different samples of milk from each of the nine combinations of incubation temperatures and media. The individual counts appearing in this table are the averages of triplicate plates. Each plate of the series of three checked with the other plates of the series as closely as would be expected from duplicate or triplicate plates from the same dilution of any sample of normal milk. In order to indicate in a comprehensive manner the variations obtained, the 37° count was taken as the standard. Any variation above or below this count is indicated by a plus or a minus sign. The variations are shown also as percentages, the 37° count being accepted as 100 per cent, and counts higher or lower being indicated by figures above or below 100.

TABLE 1. Variations in Counts Obtained by Plain and Carbohydrate Agar at Different Incubation Temperatures

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
1.....	37°	6,800,000	.....	100	11,610,000	4,810,000+	170	11,940,000	5,140,000+	173
	30°	7,080,000	280,000+	104	11,790,000	4,990,000+	173	10,580,000	3,780,000+	156
	20°	5,970,000	830,000—	88	7,550,000	750,000+	111	10,090,000	3,290,000+	148
2.....	37°	41,000	.....	100	26,400	14,600—	65	36,600	4,400—	89
	30°	41,300	300+	101	38,400	2,600—	93	38,600	2,400—	94
	20°	41,500	500+	101	34,600	6,400—	85	38,300	2,700—	93
3.....	37°	17,100	.....	100	16,000	1,100—	93	16,100	1,000—	94
	30°	21,200	4,100+	124	17,000	100—	99	18,800	1,700+	110
	20°	23,100	6,000+	135	18,700	1,600+	109	16,700	400—	98
4.....	37°	10,300	.....	100	7,100	3,200—	69	9,300	1,000—	90
	30°	14,900	4,600+	145	14,000	3,700+	136	13,100	2,800+	127
	20°	14,400	4,100+	140	12,500	2,200+	121	14,300	4,000+	139
5.....	37°	710,000	.....	100	440,000	270,000—	62	370,000	340,000—	52
	30°	980,000	270,000+	138	840,000	130,000+	118	770,000	60,000+	108
	20°	920,000	210,000+	130	970,000	260,000+	137	1,060,000	350,000+	149
6.....	37°	14,100	.....	100	14,500	400+	103	15,900	1,800+	113
	30°	18,600	4,500+	132	15,900	1,800+	113	16,300	2,200+	114
	20°	18,000	3,900+	128	15,700	1,600+	111	16,100	2,000+	116
7.....	37°	2,400,000	.....	100	1,740,000	660,000—	72	2,290,000	110,000—	97
	30°	2,950,000	550,000+	123	3,150,000	750,000+	131	3,190,000	790,000+	133
	20°	3,060,000	660,000+	127	3,120,000	720,000+	130	2,960,000	560,000+	123
8.....	37°	11,800	.....	100	18,100	6,300+	153	18,300	6,500+	155
	30°	41,700	29,900+	353	37,800	26,000+	320	36,200	24,400+	307
	20°	39,600	27,800+	336	35,600	23,800+	302	35,700	23,900+	303

9.....	37°	26,600	.....	100	35,400	8,800+	133	26,200	400—	99
	30°	30,300	3,700+	114	29,600	3,000+	111	25,300	1,300—	95
	20°	36,300	9,700+	136	27,500	900+	103	23,600	3,000—	89
10.....	37°	6,270,000	.....	100	5,490,000	780,000—	88	5,970,000	300,000—	95
	30°	5,050,000	1,220,000—	80	6,380,000	110,000+	102	7,060,000	790,000+	113
	20°	7,750,000	1,480,000+	124	6,340,000	70,000+	101	6,430,000	160,000+	103
11.....	37°	116,700	.....	100	122,100	5,400+	105	109,000	7,700—	93
	30°	110,800	5,900—	95	89,600	27,100—	77	107,500	9,200—	92
	20°	96,800	19,900—	83	80,400	36,300—	69	82,800	33,900	71
12.....	37°	1,650,000	.....	100	1,790,000	140,000+	108	1,480,000	170,000—	90
	30°	2,520,000	870,000+	153	2,260,000	610,000+	137	2,290,000	640,000+	139
	20°	2,310,000	660,000+	140	2,310,000	660,000+	140	2,220,000	570,000+	135
13.....	37°	32,000	.....	100	28,800	3,200—	90	31,600	400—	99
	30°	29,400	2,600—	93	36,200	4,200+	113	37,700	5,700+	118
	20°	42,100	10,100+	131	33,500	1,500+	105	35,700	3,700+	112
14.....	37°	830,000	.....	100	780,000	50,000—	94	860,000	30,000+	104
	30°	1,090,000	260,000+	131	960,000	130,000+	116	1,290,000	460,000+	155
	20°	1,150,000	320,000+	139	930,000	100,000+	112	1,190,000	360,000+	143
15.....	37°	278,000	.....	100	274,000	4,000—	99	307,000	29,000+	110
	30°	309,000	31,000+	111	256,000	22,000—	92	282,000	4,000+	101
	20°	324,000	46,000+	117	264,000	14,000—	95	268,000	10,000—	96
16.....	37°	8,500,000	.....	100	7,900,000	600,000—	93	8,400,000	100,000—	99
	30°	10,400,000	1,900,000+	122	8,700,000	200,000+	102	11,900,000	3,400,000+	140
	20°	9,600,000	1,100,000+	113	9,500,000	1,000,000+	112	10,400,000	1,900,000+	122
17.....	37°	12,000	.....	100	11,900	100—	99	10,100	1,900—	84
	30°	12,900	900+	107	10,800	1,200—	90	11,300	700—	94
	20°	10,700	1,300—	90	11,600	400—	97	11,600	400—	97

TABLE 1 (*continued*)

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
18.....	37°	960,000	.....	100	1,280,000	320,000+	133	990,000	30,000+	103
	30°	1,100,000	140,000+	115	1,220,000	260,000+	127	1,240,000	280,000+	129
	20°	1,090,000	130,000+	114	1,390,000	430,000+	145	1,240,000	280,000+	129
19.....	37°	154,800	.....	100	135,600	19,200—	88	148,100	6,700—	96
	30°	185,400	30,600+	120	142,600	12,200—	92	120,300	34,500—	78
	20°	182,600	27,800+	118	122,800	32,000—	79	178,700	23,900+	115
20.....	37°	660,000	.....	100	660,000	.....	100	810,000	150,000+	123
	30°	720,000	60,000+	109	600,000	60,000—	91	820,000	160,000+	124
	20°	870,000	210,000+	132	800,000	140,000+	121	860,000	200,000+	130
21.....	37°	2,100	.....	100	2,500	400+	119	2,200	100+	105
	30°	2,600	500+	124	2,100	.....	100	2,400	300+	113
	20°	2,500	400+	119	2,700	600+	129	3,400	1,300+	162
22.....	37°	8,000	.....	100	12,000	4,000+	150	18,000	10,000+	225
	30°	34,000	26,000+	425	32,000	24,000+	400	35,000	27,000+	437
	20°	16,000	8,000+	200	32,000	24,000+	400	36,000	28,000+	450
23.....	37°	2,000	.....	100	3,000	1,000+	150	1,000	1,000—	50
	30°	6,000	4,000+	300	2,000	.....	100	3,000	1,000+	150
	20°	4,000	2,000+	200	4,000	2,000+	200	1,000	1,000—	50
24.....	37°	73,000	.....	100	59,000	14,000—	81	35,000	38,000—	48
	30°	76,000	3,000+	104	93,000	20,000+	128	66,000	7,000—	90
	20°	29,000	44,000—	40	11,000	62,000—	15	15,000	58,000—	20
25.....	37°	1,200,000	.....	100	1,687,000	487,000+	140	1,150,000	50,000—	96
	30°	2,281,000	1,081,000+	190	2,304,000	1,104,000+	192	1,181,000	19,000—	98
	20°	325,000	875,000—	27	19,000	1,181,000—	2	2,003,000	803,000+	167

26.....	37°	72,000	.....	100	747,000	675,000+	1,037	1,290,000	1,218,000+	1,792
	30°	70,000	2,000—	98	651,000	579,000+	904	1,478,000	1,406,000+	2,052
	20°	62,000	10,000—	87	31,000	41,000—	43	21,000	51,000—	30
27.....	37°	60,000	.....	100	42,000	18,000—	30	47,000	13,000—	78
	30°	387,000	327,000+	645	371,000	311,000+	618	341,000	281,000+	568
	20°	358,000	298,000+	597	502,000	442,000+	837	345,000	285,000+	575
28.....	37°	80,000	.....	100	76,000	4,000—	95	105,000	25,000+	131
	30°	134,000	54,000+	167	125,000	45,000+	156	130,000	50,000+	162
	20°	127,000	47,000+	159	98,000	18,000+	122	151,000	71,000+	189
29.....	37°	102,000	.....	100	164,000	62,000+	161	243,000	141,000+	238
	30°	160,000	58,000+	157	174,000	72,000+	171	210,000	108,000+	206
	20°	215,000	113,000+	211	184,000	82,000+	180	175,000	73,000+	171
30.....	37°	3,950,000	.....	100	3,290,000	660,000—	84	2,860,000	1,090,000—	72
	30°	6,740,000	2,790,000+	170	6,280,000	2,330,000+	159	4,170,000	220,000+	105
	20°	7,260,000	3,310,000+	184	6,460,000	2,510,000+	163	650,000	3,300,000—	16
31.....	37°	520,000	.....	100	670,000	150,000+	129	1,050,000	530,000+	202
	30°	1,980,000	1,460,000+	381	1,800,000	1,280,000+	346	2,780,000	2,260,000+	534
	20°	1,680,000	1,160,000+	323	1,680,000	1,160,000+	323	1,660,000	1,140,000+	319
32.....	37°	250,000	.....	100	170,000	80,000—	68	350,000	100,000+	140
	30°	580,000	330,000+	232	630,000	380,000+	252	520,000	270,000+	208
	20°	630,000	380,000+	252	520,000	270,000+	208	410,000	160,000+	164
33.....	37°	19,000	.....	100	16,000	3,000—	84	4,000	15,000—	21
	30°	39,000	20,000+	205	43,000	24,000+	226	30,000	11,000+	158
	20°	36,000	17,000+	189	27,000	8,000+	142	28,000	9,000+	147
34.....	37°	80,000	.....	100	98,000	18,000+	122	74,000	6,000—	92
	30°	114,000	34,000+	142	122,000	42,000+	152	110,000	30,000+	137
	20°	85,000	5,000+	106	123,000	43,000+	154	97,000	17,000+	121

Table 1 (*continued*)

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
35.....	37°	106,300	.....	100	125,200	18,900+	118	131,300	25,000+	124
	30°	138,100	31,800+	130	145,200	38,900+	137	114,900	8,600+	107
	20°	133,100	26,800+	125	116,400	10,000+	109	94,900	11,400—	89
36.....	37°	30,000	.....	100	390,000	360,000+	1,300	240,000	210,000+	800
	30°	90,000	60,000+	300	40,000	10,000+	133	620,000	590,000+	2,067
	20°	60,000	30,000+	200	30,000	.....	100	320,000	290,000+	1,067
37.....	37°	10,000	.....	100	10,000	.....	100	70,000	60,000+	700
	30°	50,000	40,000+	500	10,000	.....	100	800,000	790,000+	8,000
	20°	40,000	30,000+	400	30,000	20,000+	300	610,000	600,000+	6,100
38.....	37°	20,000	.....	100	20,000	.....	100	270,000	250,000+	1,350
	30°	30,000	10,000+	150	20,000	.....	100	590,000	570,000+	2,950
	20°	30,000	10,000+	150	30,000	10,000+	150	380,000	360,000+	1,900
39.....	37°	20,000	.....	100	40,000	20,000+	200	140,000	120,000+	700
	30°	60,000	40,000+	300	20,000	.....	100	260,000	240,000+	1,300
	20°	20,000	.....	100	40,000	20,000+	200	300,000	280,000+	1,500
40.....	37°	10,000	.....	100	10,000	.....	100	60,000	50,000+	600
	30°	10,000	.....	100	10,000	.....	100	650,000	640,000+	6,500
	20°	10,000	.....	100	10,000	.....	100	40,000	30,000+	400
41.....	37°	20,000	.....	100	20,000	.....	100	150,000	130,000+	750
	30°	30,000	10,000+	150	20,000	.....	100	190,000	170,000+	950
	20°	10,000	10,000—	50	20,000	.....	100	19,000	1,000—	95
42.....	37°	510,000	.....	100	250,000	260,000—	49	420,000	90,000—	83
	30°	480,000	30,000—	94	550,000	40,000+	107	650,000	140,000+	127
	20°	480,000	30,000—	94	540,000	30,000+	106	800,000	290,000+	157

43.....	37°	10,000	.....	100	6,000	4,000—	60	340,000	330,000+	3,400
	30°	20,000	10,000+	200	40,000	30,000+	400	310,000	300,000+	3,100
	20°	10,000	.....	100	10,000	.....	100	330,000	320,000+	3,300
44.....	37°	20,000	.....	100	30,000	10,000+	150	250,000	230,000+	1,250
	30°	30,000	10,000+	150	40,000	20,000+	200	370,000	350,000+	1,850
	20°	40,000	20,000+	200	60,000	40,000+	300	400,000	380,000+	2,000
45.....	37°	21,000	.....	100	12,000	9,000—	57	61,000	40,000+	290
	30°	55,000	34,000+	262	60,000	39,000+	276	61,000	40,000+	290
	20°	31,000	10,000+	148	50,000	29,000+	238	64,000	43,000+	305
46.....	37°	27,000	.....	100	34,000	7,000+	126	89,000	62,000+	330
	30°	101,000	74,000+	374	109,000	82,000+	404	130,000	103,000+	481
	20°	112,000	85,000+	415	121,000	94,000+	448	133,000	106,000+	493
47.....	37°	19,000	.....	100	32,000	13,000+	168	69,000	50,000+	363
	30°	25,000	6,000+	132	88,000	69,000+	463	52,000	33,000+	274
	20°	53,000	34,000+	279	76,000	57,000+	400	71,000	52,000+	373
48.....	37°	10,000	.....	100	9,000	1,000—	90	12,000	2,000+	120
	30°	10,000	.....	100	14,000	4,000+	140	11,000	1,000+	110
	20°	10,000	.....	100	10,000	.....	100	17,000	7,000+	170
49.....	37°	20,000	.....	100	24,000	4,000+	120	102,000	82,000+	510
	30°	20,000	.....	100	32,000	12,000+	160	31,000	11,000+	155
	20°	20,000	.....	100	17,000	3,000—	85	32,000	12,000+	160
50.....	37°	269,000	.....	100	84,000	185,000—	31	120,000	149,000—	45
	30°	307,000	38,000+	114	267,000	2,000—	99	229,000	40,000—	85
	20°	266,000	3,000—	99	300,000	31,000+	112	332,000	63,000+	123
51.....	37°	6,000	.....	100	4,000	2,000—	67	12,000	6,000+	200
	30°	17,000	11,000+	283	9,000	3,000+	150	13,000	7,000+	217
	20°	22,000	16,000+	366	12,000	6,000+	200	28,000	22,000+	467

Table 1 (*continued*)

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
52.....	37°	75,000	.....	100	64,000	11,000—	85	143,000	68,000+	191
	30°	153,000	78,000+	204	171,000	96,000+	228	175,000	100,000+	233
	20°	149,000	74,000+	199	170,000	95,000+	227	197,000	122,000+	263
53.....	37°	86,000	.....	100	93,000	7,000+	108	172,000	86,000+	200
	30°	133,000	47,000+	155	121,000	35,000+	141	120,000	34,000+	140
	20°	134,000	48,000+	156	106,000	20,000+	123	113,000	27,000+	131
54.....	37°	82,000	.....	100	345,000	263,000+	421	369,000	287,000+	450
	30°	69,000	13,000—	84	396,000	314,000+	483	368,000	286,000+	449
	20°	76,000	6,000—	93	137,000	55,000+	167	213,000	131,000+	260
55.....	37°	6,000	.....	100	1,000	5,000—	17	16,000	10,000+	267
	30°	26,000	20,000+	433	9,000	3,000+	150	18,000	12,000+	300
	20°	8,000	2,000+	133	7,000	1,000+	117	8,000	2,000+	133
56.....	37°	26,000	.....	100	71,000	45,000+	273	73,000	47,000+	280
	30°	691,000	665,000+	2,658	830,000	804,000+	3,192	671,000	645,000+	2,581
	20°	458,000	432,000+	1,762	677,000	651,000+	2,604	497,000	471,000+	1,912
57.....	37°	102,000	.....	100	43,000	59,000—	42	69,000	33,000—	68
	30°	816,000	714,000+	800	967,000	865,000+	948	697,000	595,000+	683
	20°	1,159,000	1,057,000+	1,136	1,365,000	1,263,000+	1,338	1,653,000	1,551,000+	1,620
58.....	37°	110,000	.....	100	252,000	142,000+	229	146,000	36,000+	133
	30°	163,000	53,000+	148	341,000	231,000+	310	174,000	64,000+	158
	20°	194,000	84,000+	176	178,000	68,000+	162	110,000	.....	100
59.....	37°	56,000	.....	100	170,000	114,000+	304	357,000	301,000+	637
	30°	79,000	23,000+	141	240,000	184,000+	429	235,000	179,000+	420
	20°	109,000	53,000+	195	156,000	100,000+	279.	92,000	36,000+	164

60.....	37°	13,000	.....	100	9,000	4,000—	70	51,000	38,000+	392
	30°	26,000	13,000+	200	19,000	6,000+	146	71,000	58,000+	546
	20°	20,000	7,000+	154	20,000	7,000+	154	37,000	24,000+	285
61.....	37°	8,000	.....	100	7,000	1,000—	87	168,000	160,000+	2,100
	30°	18,000	10,000+	225	11,000	3,000+	137	106,000	98,000+	1,325
	20°	12,000	4,000+	150	11,000	3,000+	137	58,000	50,000+	725
62.....	37°	6,000	.....	100	6,000	.....	100	6,000	.....	100
	30°	12,000	6,000+	200	8,000	2,000+	133	8,000	2,000+	133
	20°	7,000	1,000+	116	6,000	.....	100	9,000	3,000+	150
63.....	37°	28,000	.....	100	15,000	13,000—	54	28,000	.....	100
	30°	31,000	3,000+	111	25,000	3,000—	89	41,000	13,000+	146
	20°	20,000	8,000—	71	31,000	7,000—	75	22,000	6,000—	79
64.....	37°	45,000	.....	100	39,000	6,000—	87	50,000	5,000+	111
	30°	42,000	3,000—	93	63,000	18,000+	140	70,000	25,000+	155
	20°	30,000	15,000—	67	48,000	3,000+	107	36,000	9,000—	80
65.....	37°	22,000	.....	100	12,000	10,000—	55	21,000	1,000—	95
	30°	33,000	11,000+	150	30,000	8,000+	136	17,000	5,000—	77
	20°	23,000	1,000+	105	18,000	4,000—	82	36,000	14,000+	164
66.....	37°	490,000	.....	100	371,000	119,000—	76	795,000	305,000+	162
	30°	1,405,000	915,000+	286	525,000	35,000+	107	459,000	31,000—	94
	20°	767	489,233—	0.1	1,123	488,877—	0.2	1,308	488,692—	0.2
67.....	37°	76,000	.....	100	95,000	19,000+	126	83,000	7,000+	109
	30°	69,000	7,000—	91	87,000	11,000+	114	96,000	20,000+	126
	20°	86,000	10,000+	113	60,000	16,000—	79	50,000	26,000—	66
68.....	37°	6,000	.....	100	3,000	3,000—	50	3,000	3,000—	50
	30°	290,000	284,000+	4,833	100,000	94,000+	1,666	180,000	174,000+	3,000
	20°	330,000	324,000+	5,500	360,000	354,000+	6,000	470,000	464,000+	7,833

TABLE 1 (*continued*)

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
69.....	37°	51,000	.....	100	56,000	5,000+	110	58,000	7,000+	114
	30°	123,000	72,000+	241	99,000	48,000+	194	105,000	54,000+	206
	20°	99,000	48,000+	194	63,000	12,000+	124	66,000	15,000+	129
70.....	37°	25,000	.....	100	30,000	5,000+	120	30,000	5,000+	120
	30°	174,000	149,000+	696	146,000	121,000+	584	124,000	99,000+	496
	20°	177,000	152,000+	708	125,000	100,000+	500	131,000	106,000+	524
71.....	37°	87,000	.....	100	120,000	33,000+	138	157,000	70,000+	180
	30°	380,000	293,000+	437	338,000	251,000+	389	322,000	235,000+	370
	20°	407,000	320 000+	469	350,000	263,000+	402	358,000	271,000+	411
72.....	37°	7,000	.....	100	3,000	4,000—	43	2,000	5,000—	29
	30°	13,000	6,000+	186	15,000	8,000+	214	7,000	.....	100
	20°	2,000	5,000—	29	5,000	2,000—	71	5,000	2,000—	71
73.....	37°	8,000	.....	100	6,000	2,000—	75	6,000	2,000—	75
	30°	12,000	4,000+	150	10,000	2,000+	125	8,000	.....	100
	20°	8,000	.....	100	8,000	.....	100	7,000	1,000—	87
74.....	37°	14,000	.....	100	12,000	2,000—	86	8,000	6,000—	57
	30°	28,000	14,000+	200	27,000	13,000+	193	17,000	3,000+	121
	20°	21,000	7,000+	150	14,000	.....	100	20,000	6,000+	142
75.....	37°	3,000	.....	100	1,000	2,000—	33	4,000	1,000+	133
	30°	6,000	3,000+	200	5,000	2,000+	167	3,000	.....	100
	20°	3,000	.....	100	2,000	1,000—	67	1,000	2,000—	33
76.....	37°	28,000	.....	100	23,000	5,000—	82	25,000	3,000—	89
	30°	91,000	63,000+	325	66,000	38,000+	235	64,000	36,000+	229
	20°	64,000	36,000+	229	66,000	38,000+	235	65,000	37,000+	234

77.....	37°	6,000	.....	100	7,000	1,000+	117	19,000	13,000+	317
	30°	1,393,000	1,387,000+	23,217	983,000	977,000+	16,383	1,077,000	1,071,000+	17,950
	20°	830,000	824,000+	13,833	1,050,000	1,044,000+	17,500	967,000	961,000+	16,117
78.....	37°	2,000	.....	100	1,000	1,000—	50	1,000	1,000—	50
	30°	8,000	6,000+	400	6,000	4,000+	300	8,000	6,000+	400
	20°	5,000	3,000+	250	3,000	1,000+	150	3,000	1,000+	150
79.....	37°	20,000	.....	100	306,000	286,000+	1,530	309,000	289,000+	1,545
	30°	105,000	85,000+	525	449,000	429,000+	2,245	333,000	313,000+	1,665
	20°	184,000	164,000+	920	442,000	422,000+	2,210	163,000	143,000+	815
80.....	37°	110,000	.....	100	100,000	10,000—	91	84,000	26,000—	76
	30°	199,000	89,000+	181	169,000	59,000+	154	132,000	22,000+	120
	20°	171,000	61,000+	155	176,000	66,000+	160	151,000	41,000+	137
81.....	37°	19,000	.....	100	373,000	354,000+	1,963	348,000	329,000+	1,831
	30°	37,000	18,000+	195	379,000	360,000+	1,994	404,000	385,000+	2,126
	20°	22,000	3,000+	116	365,000	346,000+	1,921	336,000	317,000+	1,768
82.....	37°	190,000	.....	100	130,000	60,000—	68	720,000	530,000+	379
	30°	160,000	30,000—	84	210,000	20,000+	110	320,000	130,000+	168
	20°	200,000	10,000+	105	230,000	40,000+	121	240,000	50,000+	126
83.....	37°	412,000	.....	100	417,000	5,000+	101	372,000	40,000—	90
	30°	850,000	438,000+	206	715,000	303,000+	176	975,000	563,000+	237
	20°	962,000	550,000+	233	740,000	328,000+	180	884,000	472,000+	214
84.....	37°	15,000	.....	100	15,000	.....	100	21,000	6,000+	140
	30°	58,000	43,000+	387	44,000	29,000+	295	73,000	58,000+	486
	20°	52,000	37,000+	347	31,000	16,000+	207	42,500	27,500+	283
85.....	37°	13,000	.....	100	10,000	3,000—	77	34,000	21,000+	261
	30°	23,000	10,000+	177	23,000	10,000+	177	29,000	16,000+	223
	20°	18,000	5,000+	138	14,000	1,000+	108	35,000	22,000+	269

TABLE 1 (*continued*)

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
86.....	37°	5,000	.....	100	6,000	1,000+	120	17,000	12,000+	340
	30°	8,000	3,000+	160	7,000	2,000+	140	16,000	11,000+	320
	20°	10,000	5,000+	200	7,000	2,000+	140	27,000	22,000+	540
87.....	37°	27,000	.....	100	15,000	12,000—	56	34,000	7,000+	126
	30°	191,000	164,000+	707	171,000	144,000+	633	138,000	111,000+	511
	20°	229,000	202,000+	848	161,000	134,000+	596	129,000	102,000+	478
88.....	37°	41,000	.....	100	32,000	9,000—	78	59,000	18,000+	144
	30°	319,000	278,000+	778	340,000	299,000+	829	498,000	457,000+	1,215
	20°	512,000	471,000+	1,249	774,000	733,000+	1,888	751,000	710,000+	1,832
89.....	37°	6,000	.....	100	9,000	3,000+	150	10,000	4,000+	167
	30°	59,000	53,000+	383	40,000	34,000+	667	87,000	81,000+	1,450
	20°	56,000	50,000+	933	44,000	38,000+	733	44,000	38,000+	733
90.....	37°	401,000	.....	100	468,000	67,000+	117	467,000	66,000+	116
	30°	6,000	395,000—	1	6,000	395,000—	1	19,000	382,000—	5
	20°	8,000	393,000—	2	10,000	391,000—	2	17,000	384,000—	4
91.....	37°	609,000	.....	100	751,000	142,000+	123	572,000	37,000—	94
	30°	2,497,000	1,888,000+	410	1,544,000	935,000+	253	937,000	328,000+	154
	20°	4,019,000	3,410,000+	660	5,660,000	5,051,000+	929	4,238,000	3,629,000+	696
92.....	37°	331,000	.....	100	382,000	51,000+	115	398,000	67,000+	120
	30°	434,000	103,000+	131	409,000	78,000+	124	424,000	93,000+	128
	20°	420,000	89,000+	127	357,000	26,000+	108	477,000	146,000+	144
93.....	37°	• 328,000	.....	100	282,000	46,000—	86	247,000	81,000—	75
	30°	344,000	16,000+	105	257,000	71,000—	78	378,000	50,000+	115
	20°	330,000	2,000+	101	336,000	8,000+	102	351,000	23,000+	107

94.....	37°	27,000	.....	100	23,000	4,000—	85	39,000	12,000+	144
	30°	56,000	29,000+	207	55,000	28,000+	204	83,000	56,000+	307
	20°	60,000	33,000+	222	63,000	36,000+	233	106,000	79,000+	393
95.....	37°	374,000	.....	100	325,000	49,000—	87	319,000	55,000—	86
	30°	522,000	148,000+	140	518,000	144,000+	138	504,000	130,000+	135
	20°	511,000	137,000+	137	561,000	187,000+	150	425,000	51,000+	114
96.....	37°	30,000	.....	100	30,000	.....	100	290,000	260,000+	967
	30°	30,000	.....	100	10,000	20,000—	33	100,000	70,000+	333
	20°	3,000	27,000—	10	3,000	27,000—	10	3,000	27,000—	10
97.....	37°	40,000	.....	100	130,000	90,000+	325	30,000	10,000—	75
	30°	20,000	20,000—	50	6,000	34,000—	15	100,000	60,000+	250
	20°	6,000	34,000—	15	3,000	37,000—	7	3,000	37,000—	7
98.....	37°	30,000	.....	100	200,000	170,000+	667	3,980,000	3,950,000+	13,267
	30°	40,000	10,000+	133	40,000	10,000+	133	790,000	760,000+	2,633
	20°	20,000	10,000—	67	20,000	10,000—	67	100,000	70,000+	333
99.....	37°	33,000	.....	100	55,000	22,000+	167	67,000	34,000+	203
	30°	33,000	.....	100	55,000	22,000+	167	102,000	69,000+	309
	20°	49,000	16,000+	148	59,000	26,000+	179	66,000	33,000+	200
100.....	37°	20,000	.....	100	10,000	10,000—	50	100,000	80,000+	500
	30°	30,000	10,000+	150	30,000	10,000+	150	190,000	170,000+	950
	20°	40,000	20,000+	200	40,000	20,000+	200	310,000	290,000+	1,550

TABLE 2. SUMMARY OF HIGHEST AND LOWEST COUNTS FOUND ON EACH COMBINATION OF INCUBATION TEMPERATURE AND MEDIUM

Medium, and incubation temperature (C.)	Counts expressed as per cent	Total number of highest counts	Number of counts up to 200 per cent	Number of counts up to 500 per cent	Number of counts up to 1000 per cent	Number of counts up to 5000 per cent	Number of counts up to 10,000 per cent	Total number of lowest counts*
Plain 37°.....	100.0	0	0	0	0	0	0	21
Lactose 37°...	175.3	2	1	0	0	0	0	31
Dextrose 37°..	444.9	10	6	4	2	1	1	10
Plain 30°.....	519.1	17	11	1	1	1	1	2
Lactose 30°...	453.5	11	9	2	2	0	0	2
Dextrose 30°..	778.6	22	17	11	4	2	0	1
Plain 20°.....	411.4	12	3	2	0	0	0	4
Lactose 20°...	498.5	5	3	3	1	0	0	4
Dextrose 20°..	664.8	21	13	6	3	1	0	5
Total.....	.....	100	63	29	13	5	2	80

* Twenty samples in which more than one combination of temperature and medium gave the lowest results are not included in this summary.

The results given in table 1 may be compared in several ways to show the variation obtained from each medium and incubation temperature. The writers have preferred to make comparisons on the basis of the number of highest and lowest counts found under each condition and also to compare the average percentage variation in count of all samples, regarding the 37° count on plain agar as 100 per cent. These comparisons are given in table 2, in which the outstanding features are as follows: (1) from all samples, higher counts were obtained from some other medium and temperature combination than the 37° count on plain agar; (2) of these higher counts, 63 per cent were increased twofold, 29 per cent fivefold, 13 per cent tenfold, 5 per cent fiftyfold, and 2 per cent more than a hundredfold.

Comparing the effects of incubation temperatures on all media, it was found that 50 per cent of the highest counts were obtained at 30°, 38 per cent at 20°, and 12 per cent at 37°. Of the lowest counts recorded, 6.2 per cent were obtained at 30°, 16.2 per cent at 20°, and 77.6 per cent at 37°.

The results of the various compositions of media compared at all temperatures showed that 29 per cent of the highest counts were obtained on plain agar, 18 per cent on lactose agar, and 53 per cent on dextrose agar. Of the lowest counts recorded, 33.7 per cent were obtained on plain agar, 46.2 per cent on lactose agar, and 20.1 per cent on dextrose agar.

On the basis of the 37° plain-agar count, the counts for all samples, as represented by the average percentage figures, show variations ranging from less than a twofold increase, for lactose agar at 37°, to more than a sevenfold increase, for dextrose agar at 30°.

From these data it appears that dextrose agar at 30° or 20° has distinct advantages over any of the other combinations used, for obtaining higher counts. There is comparatively little choice between plain agar at 20° and 30°, and lactose agar at the same temperatures, altho plain agar at 30° seems to have a slight advantage in the number of highest counts and the average percentage increase. The 37° counts on all of the media are decidedly unfavorable in comparison with those of the other incubation temperatures. Dextrose agar, however, has evident advantages over plain and lactose agar at this temperature. The slight difference which is found between the two latter media at 37° is in favor of the lactose agar.

Variation in counts at 37° C.

While lower bacteria counts were found at 37° than at the lower incubation temperatures, it is recognized that longer incubation periods are necessary in order to develop higher counts at the lower temperatures. At the end of forty-eight hours, the 37° counts have frequently proved higher than those resulting from similar incubation periods at the lower temperatures. An additional incubation period of two or three days, however, has always been necessary in order to develop the higher counts at these lower temperatures. On the other hand, there is usually very little increase in the 37° count after the first forty-eight-hour period. These facts might easily be interpreted to mean that forty-eight hours at 37° represents a time-temperature relationship which cannot be reduced if the greatest growth in the shortest period of time is desired. This particular temperature and incubation period may therefore be looked upon as the minimum and cannot be changed without materially affecting the usefulness of the results. The exacting demands for inspection work, which have determined the use of the 37° forty-eight-hour count, are not

operative in research work, in which the longer incubation periods and lower temperatures are generally used. These longer incubation periods at lower temperatures are used for the purpose of obtaining maximum counts where immediate results are not essential. Since this is the main object, greater variations in time or temperature may be used without affecting the results to the same degree that they would be affected by similar variations in the 37° forty-eight-hour counts.

Recognizing the importance of maintaining the correct temperature for the 37° count, an attempt was made to find out what variations in counts would result from possible differences of temperature due to piling the individual plates in a compact mass, as compared with the results obtained by so arranging the plates as to allow free circulation of air around each one. The former condition occasionally exists in any laboratory, particularly when a large number of plates must be incubated at the same time. In these experiments, the capacity of the incubator was only about half utilized. The sources of heat in the incubator were at the bottom, two and one-half inches below the temporary floor, at the top, and on two sides. Variations in temperature to which individual plates might be exposed, therefore, would be due to the slow diffusion of the heat resulting from the diminished ventilation around the piles of plates.

For these comparisons, two samples of market milk containing approximately the same number of bacteria, and with no apparent differences in flora, were selected. A sufficient volume of a single dilution was made so that about 200 plates could be prepared from the same bottle. The samples were diluted with the object of obtaining between 30 and 400 colonies to the plate. All plates were poured from the same batch of plain agar. They were placed in the incubator so that consecutive numbers would lie next to each other. The average of the counts from plates bearing two consecutive numbers was considered as the count for a single sample.

In testing the effect of the free circulation of air during incubation, 200 plates were arranged in layers on wire screens with about one-half inch air space between each layer. The bottom layer was one and one-half inches from the floor of the incubator. A uniform temperature of 37° at two inches from the top, and the usual ventilation of the incubator were maintained thruout the forty-eight-hour period. The counts obtained from these samples are shown in table 3.

TABLE 3. BACTERIA COUNTS OBTAINED FROM 100 SAMPLES OF THE SAME MILK WHEN AIR HAD CIRCULATED FREELY AROUND EACH PLATE DURING INCUBATION

Sample	Bacteria per cubic centimeter	Sample	Bacteria per cubic centimeter
1	240,000	51	225,000
2	235,000	52	240,000
3	250,000	53	255,000
4	250,000	54	185,000
5	285,000	55	240,000
6	315,000	56	365,000
7	270,000	57	245,000
8	200,000	58	265,000
9	260,000	59	245,000
10	280,000	60	150,000
11	235,000	61	230,000
12	260,000	62	215,000
13	200,000	63	305,000
14	170,000	64	245,000
15	225,000	65	175,000
16	190,000	66	275,000
17	345,000	67	195,000
18	215,000	68	275,000
19	260,000	69	275,000
20	155,000	70	275,000
21	205,000	71	245,000
22	200,000	72	145,000
23	270,000	73	275,000
24	160,000	74	115,000
25	210,000	75	205,000
26	185,000	76	240,000
27	225,000	77	170,000
28	300,000	78	340,000
29	285,000	79	215,000
30	275,000	80	225,000
31	295,000	81	210,000
32	195,000	82	255,000
33	290,000	83	275,000
34	195,000	84	270,000
35	215,000	85	255,000
36	305,000	86	270,000
37	245,000	87	195,000
38	300,000	88	125,000
39	210,000	89	270,000
40	270,000	90	225,000
41	280,000	91	200,000
42	295,000	92	200,000
43	155,000	93	220,000
44	250,000	94	315,000
45	205,000	95	210,000
46	280,000	96	230,000
47	180,000	97	200,000
48	205,000	98	250,000
49	205,000	99	270,000
50	155,000	100	350,000

In testing the effect of piled plates, the procedure was as follows: Piles of 12 plates each were arranged in a solid block, 6 piles long and 3 piles wide, and containing, in all, 216 plates. The same uniformity of temperature at two inches from the top, and the same ventilation, were maintained in the incubator as in the first experiment. Likewise, the average of the counts of two adjacent plates in each pile was taken as the count for a single sample. The two bottom plates in each pile are not included in the results, as it was desirable to consider only the counts from the plates kept at the same distance from the bottom of the incubator as were those in the first experiment; therefore the results are given for only five samples to the pile. In table 4, which is constructed to show the relative position of each pile in the block, appear the results obtained for each sample, that is, the average of each two adjacent plates.

TABLE 4. BACTERIA COUNTS OBTAINED FROM SAMPLES OF THE SAME MILK WHEN PLATES WERE PILED IN A SOLID BLOCK DURING INCUBATION

Pile 1	Pile 2	Pile 3	Pile 4	Pile 5	Pile 6
424,000	402,000	366,000	338,000	404,000	456,000
419,000	346,000	336,000	403,000	358,000	366,000
419,000	395,000	303,000	339,000	402,000	397,000
368,000	367,000	272,000	345,000	360,000	364,000
328,000	308,000	210,000	191,000	152,000	302,000
Average 392,000	364,000	297,000	323,000	335,000	377,000
Pile 7	Pile 8	Pile 9	Pile 10	Pile 11	Pile 12
400,000	364,000	360,000	319,000	307,000	331,000
369,000	316,000	235,000	313,000	318,000	306,000
393,000	373,000	79,000	245,000	290,000	348,000
354,000	157,000	35,000	126,000	33,000	323,000
350,000	15,000	7,000	9,000	11,000	309,000
Average 373,000	245,000	143,000	202,000	192,000	323,000
Pile 13	Pile 14	Pile 15	Pile 16	Pile 17	Pile 18
409,000	344,000	403,000	361,000	357,000	344,000
350,000	356,000	364,000	397,000	401,000	341,000
375,000	240,000	371,000	342,000	302,000	408,000
380,000	371,000	295,000	283,000	201,000	315,000
306,000	386,000	237,000	211,000	309,000	286,000
Average 364,000	339,000	334,000	319,000	294,000	339,000

The results given in tables 3 and 4 show some striking facts concerning the effect upon the counts of these two different methods of exposure of the plates to the uniform conditions of temperature and ventilation maintained in the incubator. In table 4 there is a marked difference in the results from all top samples and samples in the corner piles, as compared with those from the bottom of the piles and particularly from those at the bottom of the piles on the inside of the block. In order to show these variations in counts, the standard deviation, the coefficient of variability, and the probable error were calculated for the entire number of samples in each set and for certain groups of samples which were packed in the solid block. These mathematical expressions are shown in table 5.

TABLE 5. VARIATIONS IN COUNTS DUE TO METHODS OF PILING PLATES AS SHOWN BY COEFFICIENT OF VARIABILITY, STANDARD DEVIATION, AND PROBABLE ERROR

Samples used for calculations	Number of samples	Average count	Standard deviation	Probable error	Coefficient of variability (per cent)
Air space between all plates (table 3)	100	237,350*	±49,014*	33,059*	20.6
Plates in solid block, all samples (table 4)	90	307,000	±105,000	70,822	34.2
Samples in corner piles only (Nos. 1, 6, 13, 18)	20	368,000	±45,485	30,679	12.3
Samples in side piles only (Nos. 2, 3, 4, 5, 7, 12, 14, 15, 16, 17)	50	330,000	±64,000	43,168	19.4
Samples in center piles only (Nos. 8, 9, 10, 11)	20	195,000	±138,016	91,742	69.7
Samples from top plates of each pile	18	365,000	±39,200	26,440	10.7
Samples from bottom plates of each pile	18	201,000	±123,200	83,098	61.3

*Not comparable with corresponding figures from samples shown in the remainder of the table because of difference in bacterial content of the milk.

The significant figures in table 5 are those representing the coefficient of variability, altho the other figures contribute toward a more comprehensive understanding of the variations found in the different groups of samples. The coefficient of variability obtained from samples when a free circulation of air was allowed between the plates was 20.6 per cent; whereas this

variability was increased to 34.2 per cent from samples that were piled in a solid block. This variation of 34.2 per cent is the resultant of larger and smaller variations from compound groups of the entire block of plates. The coefficients of variability of 10.7 per cent and 12.3 per cent from samples on the tops of all piles and from all plates in the corner piles, respectively, when compared with the higher coefficients of variability of 19.4 per cent, 69.7 per cent, and 61.3, per cent from those samples in positions less favorably situated, certainly indicate an important consideration in judging the reliability of the 37° count.

In order to determine to what extent variations in temperature within the solid block of plates were responsible for discrepant counts, an attempt was made to obtain temperature records at different places in the pile with a recording thermometer. In the absence of a more delicate apparatus, temperatures were determined with a Tycos recording instrument. All necessary precautions were observed in order to duplicate the normal temperature conditions from which the foregoing counts were obtained. These records, showing the temperature for each hour until the desired temperature of 37° was reached, are shown in table 6. Determination 1 is made from the empty incubator at a point midway between the top and the bottom; determination 2 was made under the same conditions except that the bulb of the thermometer was placed inside a petri plate; determination 3 was obtained with the bulb inside the fifth plate from the bottom of a single pile of 12 plates; determination 4 was the result of having the bulb inside the fifth plate from the bottom of a pile corresponding to pile 13 in the block of plates shown in table 4; determinations 5 and 6 were produced from plates in the same position in piles corresponding to numbers 15 and 8, respectively, of the same table. The vertical distance from the top of the incubator to the plate containing the thermometer bulb is the same as that to one of the plates included in determining the average count of the fourth ample from the top.

TABLE 6. TEMPERATURES RECORDED EACH HOUR AT DIFFERENT PLACES IN A BLOCK OF TIGHTLY PACKED PETRI PLATES

(In degrees centigrade)

Determination	Temperature at start	Temperatures recorded after								
		1 hour	2 hours	3 hours	4 hours	5 hours	6 hours	7 hours	8 hours	9 hours
1	20.0°	35.0°	37.0°	.....	.....	.....	.....	.....	.....	.....
2	20.5°	35.5°	37.0°	.....	.....	.....	.....	.....	.....	.....
3	20.5°	31.0°	34.4°	36.0°	37.0°	.....	.....	.....	.....	.....
4	21.5°	29.4°	33.8°	35.5°	36.6°	37.0°	.....	.....	.....	.....
5	21.0°	27.0°	31.6°	33.8°	35.0°	35.5°	35.5°	36.0°	36.6°	37.0°
6	21.0°	25.0°	28.0°	31.0°	32.7°	34.4°	35.5°	35.5°	36.0°	37.0°

The temperature records clearly indicate the relative length of time required by plates in different positions to reach the normal temperature. If records from inside the block of plates could have been obtained readily, it is quite probable that the length of time necessary to reach 37° would have proved even greater than that shown by determination 6. The rapidity of the heat diffusion apparently did not suffice to heat the entire block of plates soon enough to prevent marked irregularities in the counts made from the inner piles of the block. This fact emphasizes the greater likelihood of discrepant results from overcrowded incubators, or from other causes which in any way reduce the ventilation around the interior plates. In the positions represented by determinations 5 and 6, the temperatures were below normal for nine hours. This period, during which the plates in these positions were below normal, amounts to approximately 19 per cent of the entire incubation period. Plates on the outside of the pile, however, remained below normal temperature for a much shorter period, and consequently their counts were much higher and more nearly uniform than those obtained from plates that had not been maintained at the normal temperature for the entire period.

Discussion

The wide range of variations in the counts obtained by different incubation temperatures and media emphasizes the inadequacies of any single combination of temperature and media for determining the maximum

bacteria counts from miscellaneous samples of milk. Plain agar at 37° for forty-eight hours is unquestionably the least favorable combination for this purpose; the use of lactose agar at this temperature appears to have few, if any, advantages over plain agar; and altho dextrose agar at 37° has distinct advantages over those media, nevertheless the majority of the results obtained from it are lower than those produced at 20° or 30° for five days.

For developing the maximum counts, dextrose agar at 30° for five days seems to be superior to any of the other combinations considered in this paper. This medium at 20° for five days is also preferable to plain or lactose agar at either 30° or 20°. The same lack of a distinct superiority of one of these latter two media over the other exists at the lower temperatures, as well as at 37°.

Counts obtained at 37° after forty-eight hours are probably subject to greater discrepancies than those obtained at the lower temperatures for longer periods of time. It has been shown that the normal variations in temperature thruout a mass of tightly packed plates is sufficient to cause as high as a fiftyfold variation from the same sample of milk; whereas only a threefold variation was found when the plates were arranged to allow a free circulation of air around each one. To avoid gross discrepancies, it is necessary, on the basis of the previous results, to provide such ventilation in 37° incubators as will heat each individual plate in a block at an approximately equal rate.

Possible variations in bacteria counts resulting from the present plate method of enumeration should not be considered as a condition eliminating their usefulness. Bacteria counts, together with the discrepancies to which they are subject, should be considered only with full knowledge of their limitations and of the fact that they constitute but one item of the evidence necessary to grade milk into distinct classes according to its wholesomeness and keeping quality.

In order to harmonize these variations with existing numerical bacterial standards, it is essential that all factors tending to cause variations and discrepancies be reduced to a minimum. Furthermore, results obtained from such manipulations, even tho necessitating the statement of fixed numbers, should be interpreted in a manner which recognizes the lack of intrinsic value of these numbers for denoting such exact degrees of bacterial quality as the statement of fixed numerical expressions implies.

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ATTACHMENT OF THE ABDOMEN TO THE THORAX IN DIPTERA

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CONTENTS

ATTACHMENT OF THE ABDOMEN TO THE THORAX IN DIPTERA

ATTACHMENT OF THE ABDOMEN TO THE THORAX IN DIPTERA[1]

BENJAMIN P. YOUNG

Many excellent studies have been made by various investigators on the morphology of the thoracic sclerites of different groups of insects. A number of these investigators have covered the entire class Insecta with the hope of determining the ground plan on which a typical thoracic segment is based. Such investigators have done much toward establishing a uniform terminology for this particular part of insect anatomy. Other workers have limited themselves to the consideration of a smaller group, as the order or the family. But in no place in the literature has the writer been able to find a record of extensive studies on the order Diptera. Snodgrass (1909, a and b) and Crampton (1909) have each figured two species; others have made even briefer references to the group. As for comprehensive work on the relation of the anterior abdominal sclerites to those of the metathorax, nothing has been found, isolated text figures being the only contributions along this line.

Through this study, which had as its primary aim the homologizing of the abdominal and thoracic sclerites in species of each available family of the Diptera, it was hoped that something might be added to the morphological literature of the group. Among the indices to phylogeny, wing venation has come to be regarded as one of the most valuable because it is the most evident; the morphology of the genitalia has not been used as much because of the difficulties attending such studies, but at present it is gaining favor because of the desirability of using all available means in throwing light on the above-mentioned problem. Vestiture has been made use of, especially by dipterologists, but mostly for generic and specific characters. If the external morphology of this particular part of the exoskeleton can contribute but its share toward the history of the descent of the group, the writer will feel that his efforts have not been in vain.

Furthermore, systematists of the order are not in accord as to the

[1] This investigation was suggested by, and carried on under the direction and supervision of, Dr. O. A. Johannsen. The writer is indebted to him not only for many suggestions growing out of his experience with the order Diptera as a whole, but also for his sincere interest shown throughout the progress of the work.

number of abdominal segments in different families. Some have counted only definitive segments and used such for key characters, while others have taken into consideration the true number as indicated by the spiracles. One of the reasons for figuring herein the pleurites of the meso- and the metathorax and the sclerites of the proximal abdominal segments of some of the commoner species of fifty-seven families of this order, is to aid in bringing about uniformity in interpretation.

Having studied but a few species of each family, the writer cannot say that the characters of the one figure hold throughout the family, but nevertheless a typical species should afford external facies more or less characteristic of the family.

METHODS AND TECHNIQUE

Practically all of this study was made from dried specimens which had been soaked for from three hours to seven days in a 10-per-cent solution of potassium hydroxide. Some forms were already clear enough for study but were allowed to remain in the clearer for a few hours in order to relax them sufficiently for study and handling. The specimens were then washed in distilled water to which a few drops of acetic acid had been added, and preserved in 70-per-cent alcohol.

It was soon found impossible to see sutures in some forms, especially the smaller species, without dissection, and it was only after each form had been halved by a median longitudinal cut with a scalpel that the work progressed with dispatch. This operation, which was done under 70-per-cent alcohol, was followed by the removal of the viscera of each half, but during the latter operation close attention was given also to the tracheal branches leading to the spiracles in order to learn the position and number of these in the abdomen. The left half was then available for external study, while the right was reserved for internal study of phragmas, apodemes, and apophyses as an aid to the more definite location of sclerites.

The binocular microscope was used both in making dissections and for the study of specimens in 70-per-cent alcohol. Drawings were made on coordinate paper with the aid of an ocular micrometer laid off in squares. To insure the object's remaining in the same place, a small piece of plasticine, used in modeling, was stuck to the bottom of a watch glass and the fly was held against the bottom of the glass by means of two bent pins

stuck into the plasticine just above each end of the insect. For drawings requiring two or three hours this proved to be a very satisfactory method, as the alcohol remains clear for that length of time.

In each drawing an attempt was made to show all chitinized areas clear and all membranes stippled. There are sclerites to be found, however, in which it is difficult to class the integument as either chitinous or membranous. Assuming the membranous state to be the more primitive, increasing amounts of chitin laid down in membrane were represented by a decreasing amount of stippling, that is, by placing the dots farther and farther apart. All outlines, as well as sutures (using the term in a general sense), were shown in full lines, while all endoskeletal parts, such as phragmas, and all sutures covered over by other parts, such as appendages, were shown in the dot-and-dash line. In most figures the amount of development of the phragma between the meso- and the metatergum also was represented in this manner. Indistinct sutures and boundaries of chitinized areas which shade off into membrane, or vice versa, were represented by dotted lines. Spiracular openings were shown either with a crosshatched interior or with a fringed border.

Pencil drawings were inked on the coordinate paper and plates were made directly from these. Drawings were either enlarged or reduced in order that all plates might have one dimension, the length, uniform. Prints were made on contrast paper and the sclerites were labeled on these reproductions.

MATERIAL

The material on which this paper is based was all drawn from the collections in the Department of Entomology at Cornell University. Dissections have been preserved in alcohol and retained for reference.

For the convenience of systematists the figures are arranged in the order of the families to which each species belongs, as listed in Aldrich's *Catalogue of North American Diptera.*

Of the fifty-nine families according to Aldrich, one or more species from fifty-five have been studied and figured. In addition *Sciara ochrolabis* and *Piophila casei*, which are included by Aldrich under the families Mycetophilidae and Sepsidae, respectively, are figured and placed in the families Sciaridae and Piophilidae. The following families are not represented: Acanthomeridae, Apioceridae, Phycodromidae, and Nycteri-

biidae. The list which follows gives the family, the species, the sex, and a reference to the drawings made of each. In addition, information gathered during the study as to the number of abdominal spiracles and their location in membrane or chitin is included.

Order *Diptera*

Division *Proboscidae*

Orthorrhapha — Nemocera

Tipulidae. *Pedicia albivitta*, female (Plate IX, 1 and 2), eight abdominal spiracles, all but last in membrane. It is possible that the supposed eighth spiracle may be the caudal attachment of the tracheal system to the tergite.

Pachyrrhina ferruginea, male (Plate IX, 3), seven abdominal spiracles, all in membrane.

Rhyphidae. *Trichocera brumalis*, female (Plate X, 4), seven abdominal spiracles, all in membrane.

Dixidae. *Dixa modesta*, female (Plate X, 5), seven abdominal spiracles, all in membrane.

Psychodidae. *Psychoda slossoni*, female (Plate X, 6), seven abdominal spiracles, all in membrane.

Chironomidae. *Chironomus ferrugineavitta*, male (Plate XI, 7 and 8), at least seven and possibly eight abdominal spiracles, all in membrane.

Culicidae. *Culex canadensis*, male (Plate XI, 9), seven abdominal spiracles, all in membrane.

Anopheles quadrimaculata, female (Plate XII, 10), seven abdominal spiracles, all in membrane.

Corethra albipes, female (Plate XII, 11), seven abdominal spiracles, all in membrane.

Mycetophilidae. *Leia winthemi*, female (Plate XII, 12), seven abdominal spiracles, all in membrane.

Sciaridae. *Sciara ochrolabis*, male (Plate XIII, 13), seven abdominal spiracles, all in membrane.

Cecidomyiidae. *Rhabdophaga strobiloides*, male (Plate XIII, 14), seven abdominal spiracles, all in membrane.

Bibionidae. *Plecia heteroptera*, female (Plate XIII, 15), eight abdominal spiracles, all in membrane.

Simuliidae. *Simulium hirtipes*, male (Plate XIV, 16), seven abdominal spiracles, all but first in membrane.

Blepharoceridae. *Blepharocera tenuipes*, female (Plate XIV, 17), seven abdominal spiracles, all in membrane.

Crphnephilidae. *Orphnephila americana*, female (Plate XIV, 18), seven abdominal spiracles, all in membrane. Semblance of eighth spiracle indicated by color but no spiracular opening to be seen.

Orthorrhapha — Brachycera

Stratiomyiidae. *Allognosta fuscitarsis*, female (Plate XV, 19), seven abdominal spiracles, all in membrane.

Tabanidae. *Chrysops indus*, male (Plate XV, 20), seven abdominal spiracles, all in membrane.

Leptidae. *Chrysopila ornata*, male (Plate XV, 21), seven abdominal spiracles, all in membrane.

Nemistrinidae. *Hirmoneura* sp., female (Plate XVI, 22), seven abdominal spiracles, all in membrane.

Cyrtidae. *Oncodes incultus*, female (Plate XVI, 23), six abdominal spiracles, all in chitin.

Bombylidae. *Anthrax alternata*, female (Plate XVI, 24), seven abdominal spiracles, all in membrane.

Therevidae. *Thereva fucata*, male (Plate XVII, 25), seven abdominal spiracles, all in membrane.

Scenopinidae. *Scenopinus fenestralis*, female (Plate XVII, 26), at least seven and possibly eight abdominal spiracles, probably all in membrane, although those of last four segments (considering eight spiracles) are very close to the chitinous margin of the sternites.

Midaidae. *Midas clavatus*, female (Plate XVII, 27), eight abdominal spiracles, all in membrane except last which is surrounded by chitin.

Asilidae. *Leptogaster loewi*, female (Plate XVIII, 28), at least seven and possibly an eighth abdominal spiracle, all except eighth in membrane.

Dolichopodidae. *Dolichopus cuprinus*, male (Plate XVIII, 29), seven abdominal spiracles, all in membrane.

Empididae. *Rhamphomyia* sp., female (Plate XVIII, 30), seven abdominal spiracles, all in membrane.

Lonchopteridae. *Lonchoptera* sp., female (Plate XIX, 31), seven abdominal spiracles, last four in membrane.

Phoridae. *Phora concinna*, female (Plate XIX, 32), at least six and possibly seven abdominal spiracles, all in membrane.

yclorrhapha — Athericera

Platypezidae. *Platypeza velutina*, female (Plate XIX, 33), seven abdominal spiracles, first, fifth, sixth, and seventh in membrane.

Pipunculidae. *Pipunculus atlanticus*, female (Plate XX, 34), seven abdominal spiracles, all in membrane.

Syrphidae. *Syrphus americanus*, male (Plate XX, 35), seven abdominal spiracles, all in membrane.

Conopidae. *Myopa vesiculosa*, male (Plate XX, 36), seven abdominal spiracles, all but sixth and seventh in membrane.

yclorrhapha — Calyptratae

Oestridae. *Gastrophilus intestinalis*, female (Plate XXI, 37), seven abdominal spiracles, all in membrane.

Tachinidae. *Tachina mella*, female (Plate XXI, 38), seven abdominal spiracles, sixth only in membrane although first is in very light chitin.

Dexiidae. *Thelaira nigripes*, male (Plate XXI, 39), seven abdominal spiracles, probably all in chitin although first, sixth, and seventh are in very light chitin.

Sarcophagidae. *Sarcophaga communis*, male (Plate XXII, 40), seven abdominal spiracles, first and sixth alone in membrane.

Muscidae. *Muscina stabulans*, female (Plate XXII, 41), seven abdominal spiracles, first, sixth, and seventh only in membrane.

Anthomyiidae. *Macrorchis ausoba*, male (Plate XXII, 42), seven abdominal spiracles, all in chitin.

Chortophila cilicrura, male (Plate XXIII, 43), seven abdominal spiracles, first and sixth in membrane.

Hylephila paludis, female (Plate XXIII, 44), seven abdominal spiracles, first, sixth, and seventh in membrane.

Schoenomyza dorsalis, female (Plate XXIII, 45), apparently only five abdominal spiracles, all in chitin. Small species, caudal spiracles may have been overlooked.

Ophyra leucostoma, male (Plate XXIII, 46), seven abdominal spiracles, first and sixth only in membrane.

Lispa sociabilis, female (Plate XXIII, 47), but five abdominal spiracles, first only in membrane.

Limnophora aequifrons, male (Plate XXIII, 48), seven abdominal spiracles, sixth only in membrane.

Eremomyia cylindrica, female (Plate XXIV, 49), seven abdominal spiracles, first only in membrane, although last two, which are rather close together, penetrate very light chitin.

Pegomyia affinis, female (Plate XXIV, 50), seven abdominal spiracles, first only in membrane, although last two, which are close together, penetrate very light chitin.

Hylemyia lipsia, female (Plate XXIV, 51), seven abdominal spiracles, first only in membrane, although sixth and seventh are located very close together in the weak chitin of the first telescoped segment of the ovipositor.

Anthomyia radicum, male (Plate XXIV, 52), seven abdominal spiracles, first and sixth in membrane.

Hebecnema umbratica, female (Plate XXIV, 53), but five abdominal spiracles found, first only in membrane.

Fannia canicularis, male and female, seven abdominal spiracles, first only in membrane.

Cyclorrhapha — Acalyptratae

Scatophagidae. *Scatophaga stercoraria*, male (Plate XXV, 54), seven abdominal spiracles, first and seventh in membrane.

Heteroneuridae. *Clusia lateralis*, female (Plate XXV, 55), seven abdominal spiracles, first five in membrane.

Helomyzidae. *Leria serrata*, male (Plate XXV, 56), seven abdominal spiracles, all in membrane.

Borboridae. *Borborus equinus*, female (Plate XXVI, 57), seven abdominal spiracles, all in membrane.

Sciomyzidae. *Dictya umbrarum*, female (Plate XXVI, 58), seven abdominal spiracles, all but last two in membrane.

Sapromyzidae. *Sapromyza lupulina*, male (Plate XXVI, 59), seven abdominal spiracles, all in membrane.

Ortalidae. *Rivellia viridulans*, female (Plate XXVII, 60), seven abdominal spiracles, all but last in membrane.

Rhopalomeridae. *Rhopalomera flaviceps*, female (Plate XXVII, 61), seven abdominal spiracles, all in membrane.

Trypetidae. *Euaresta festiva*, female (Plate XXVII, 62), seven abdominal spiracles, all but last in membrane.

Micropezidae. *Calobata albiceps*, female (Plate XXVIII, 63), seven abdominal spiracles, all but last in membrane.

Sepsidae. *Sepsis violacea*, female (Plate XXVIII, 64), seven abdominal spiracles, all but last two in membrane.

Piophilidae. *Piophila casei*, female (Plate XXVIII, 65), seven abdominal spiracles, all in membrane.

Psilidae. *Loxocera pleuritica*, male (Plate XXIX, 66), seven abdominal spiracles, all in membrane.

Diopsidae. *Sphyracephala brevicornis*, female (Plate XXIX, 67), seven abdominal spiracles, all in membrane.

Ephydridae. *Parydra limpidipennis*, female (Plate XXIX, 68), six abdominal spiracles, first only in membrane.

Oscinidae. *Chlorops* sp., male (Plate XXX, 69), six abdominal spiracles, first, second, and sixth only in membrane.

Drosophilidae. *Drosophila melanogaster* (*?*), female (Plate XXX, 70), seven abdominal spiracles, all in membrane.

Geomyzidae. *Anthomyza gracilis*, female (Plate XXX, 71), six abdominal spiracles found, all in membrane. Specimen so small that it was hard to be sure of no seventh spiracle.

Agromyzidae. *Agromyza lateralis*, male (Plate XXXI, 72), seven abdominal spiracles, all but last two in membrane. In female of species all but last one of seven spiracles are in membrane.

Division *Eproboscidae*

Hippoboscidae. *Melophagus ovinus*, female (Plate XXXI, 73), seven abdominal spiracles, all in membrane.

Olfersia americana, female (Plates XXXI, 74, and XXXII, 75), seven abdominal spiracles, all in membrane.

Order *Mecoptera*

Panorpidae. *Panorpa venosa*, female (Plate XXXII, 76), eight abdominal spiracles, all in membrane.

TERMINOLOGY

The rule of priority in the selection of anatomical terms is recognized in this paper only to the extent that these are descriptive of the parts to which they refer, or else have been so generally accepted by workers

in the group that the use of another more descriptive term would add to the confusion already existing in the nomenclatures of different orders of insects.

Full lines representing sutures in drawings are not limited to any one kind of suture, but to sutures in general, whether these are spaces between approximated sclerites or plates of the integument, impressed lines, or lines formed by the approximated lips of an infolding of the body wall.

GENERALIZATIONS

The scope of this investigation makes it necessary to limit the discussion of homologies to the metathorax and the first few abdominal segments; consequently many interesting modifications and details of structure in the remaining thoracic segments which have been figured may prove of advantage to those interested in the order, but must be disregarded at present by the writer. However, sclerites have been named in the mesothorax according to the dictates of this study, and a short discussion of the terms employed will of necessity be given.

If the Apterygote are to be considered the most generalized insects (forms in which wings were never present and therefore forms in which the muscular tension and mechanical stimulus due to the proper functioning of these locomotor appendages has never been experienced), and a thoracic segment of such an insect in which there is practically no chitin laid down in the membrane is to be considered as rather primitive, then our conclusion must be that a membranous condition must have been that of the thoracic segments of primitive insects, and only when the development of appendages gave rise to muscular stresses and strains and friction of parts was it necessary that their walls should be strengthened by the deposition of chitin in their integument. All theories to the origin of insects from annelid-like ancestors tend to strengthen this hypothesis. *Panorpa venosa* (Plate XXXII, 76), therefore, has been figured simply to show the appearance of a more primitive winged form. The development of wings has meant the chitinization of terga and pleura, together with the invagination of the body wall to form the pleural ridges, while the increase in size of the legs has meant their chitinization and their division into the true coxae and mera. The straightness of the pleural and coxal ridges is a mark of primitiveness. The large amount of membrane in the abdomen is another, while the distinctiveness of the basalares and the subalares might be considered a third. The two divisions of each tergum of the

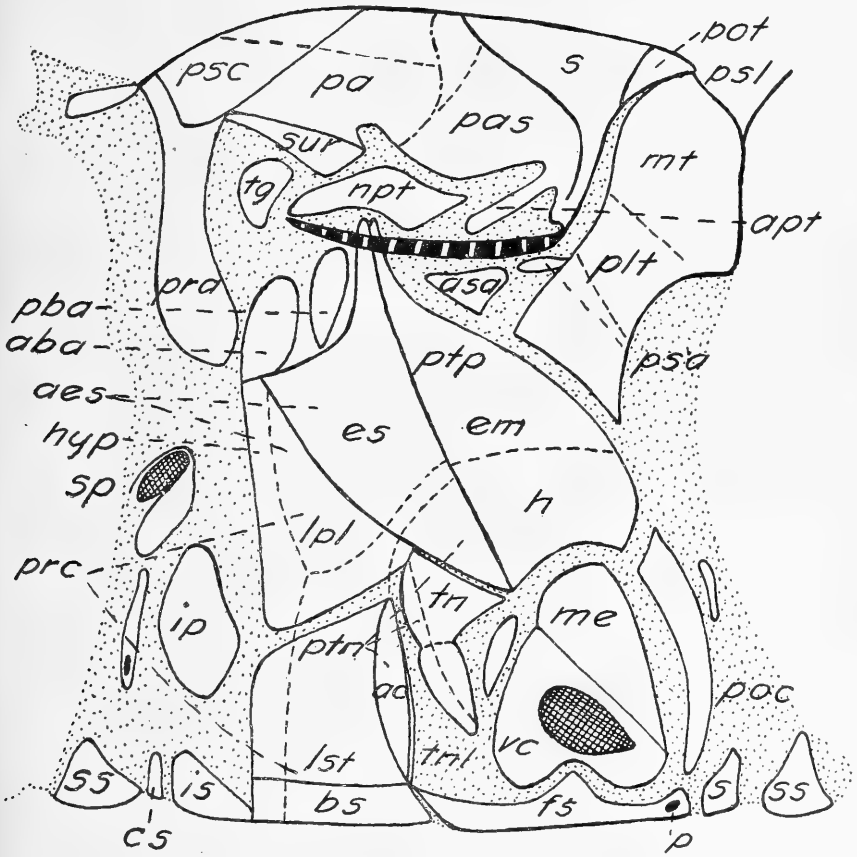

FIG. 21. GROUND PLAN OF A TYPICAL THORACIC SEGMENT IN WINGED INSECTS
(After Crampton, 1914_b)

meso- and the metathorax are clearly set off from each other, while the beginning in the development of phragmas is seen in both the anterior and the posterior infolding of the walls of the terga of these two thoracic segments. The maximum development of phragmas can be seen in the posterior mesothoracic and the anterior metathoracic one in some dipterous species.

For convenience in comparing, a copy of Crampton's (1914 b) " ground plan of a typical thoracic segment in winged insects " is here inserted (fig. 21). In the author's own words, this figure

represents an hypothetical composite type, to which the thoracic segments of any insect can be referred as a basis of comparison, rather than an attempted reconstruction of the original condition of the thoracic sclerites in the ancestors of winged insects. Most of the primitive features, however, are included in the figure, and to these have been added conditions found in the more specialized insects.

DISCUSSION OF PARTS

The mesothorax

The tergum

The two plates of the tergum as described by Verhoeff (1902) and by Snodgrass (1909 a) are readily distinguished in all forms figured. The large anterior plate, extending backward and including the axillary cord of Snodgrass (1909 b) and the post-tergite of Crampton (1914 b), composed largely of the scutum and the scutellum, has been called the scuto-scutellum when there are no visible divisions. Audouin (1824) has been followed herein in his divisions of the scuto-scutellum. The most anterior median region is termed the prescutum. The large central region, which is very often fused with the prescutum and also often subdivided by secondary sutures, is called the scutum. Laterally this division carries both the anterior and the posterior notal wing processes of Snodgrass, both of which are usually well defined in Diptera. The third division, known as the scutellum, is fairly constant as a narrow elevated median plate extending laterally into a narrow band bearing the axillary cord, which is continuous with the anal margin of the wing.

The small caudal division of the tergum when not divided is termed the postscutellum. This plate is often divided by sutures into a median and one or two lateral sclerites. When such is the case, only the abbreviations for these divisions appear on the drawings. For the middle plate the term *meditergite* (mt), and for the lateral plate or plates the term *pleuro-*

tergite (plt), are used. These are the terms which Crampton appropriates from Martin. In case there are two lateral plates formed, the writer has prefixed *ana* and *kata* to the term *pleurotergite* for the upper and lower subdivisions, respectively, calling the upper one *anapleurotergite* (aplt) and the lower one *katapleurotergite* (kplt).

The anterior phragma (Plate XXXII, 76, phg^2_a), or internal fold of the terga between the pro- and the mesothorax, is usually poorly developed in this group, and for this reason it is not indicated in the drawings. When present it usually projects under the pronotum. The posterior phragma (Plate XXXII, 76, phg^2_p) is well developed in the Brachycera (Plates XV, 21, and XVI, 24). Very frequently the two lamellae, the one of the mesonotum and the other of the metanotum, are easily distinguishable in the composition of this phragma.

The pleuron

Primarily the pleuron plate is composed of two sclerites, the episternum (es^2) and the epimeron (em^2). The suture (pleural) formed by a more or less transverse infolding of the walls of this plate (Plates IX, 1, and XI, 8, ap^2) divides it into an anterior part, the episternum, and a posterior region, the epimeron. This suture in its primitive condition extends from the wing process to the coxa, but in some of the higher Diptera, as *Muscina stabulans* (Plate XXII, 41), it may disappear altogether just above the leg. The primitive straightness of this suture as shown in *Panorpa venosa* (Plate XXXII, 76), in the Tipulidae (Plate IX, 3), in the Rhyphidae (Plate X, 4), in the Culicidae (Plate XII, 10), and in other forms, gives way in the more specialized members of the group to a prominent forward bending, in some cases, about midway dorsad from its origin at the coxa (Plates XX, 35, and XXII, 42).

Secondary sutures may divide either the episternum or the epimeron, or both, into a dorsal and a ventral region, and in some cases the dorsal episternal area into an anterior and a posterior part. If common usage did not dictate differently, the writer would prefer to use the more descriptive prefixes *ana* and *kata* combined with the names of the primary sclerites in referring to these secondary divisions, and simply refer to the secondary division of the dorsal episternum as the *anterior anepisternum*. But because of their widespread acceptance by systematists of this group, the use of Osten-Sacken's (1884) terms *pteropleura* and *sternopleura* —

slightly modified to *pteropleurite* (ptp^2) and *sternopleurite* (stp^2) as suggested by Crampton (1914 b) for *anepimeron* and *katepisternum*, respectively — seems advisable. Furthermore, Crampton's term *hypoepimeron* (hem^2) has been accepted on the same grounds. This leaves only the anepisternum to retain the more descriptive name, its anterior part being labeled "aes_a^2" and its posterior part when present being referred to as "aes_p^2".

The generalized type of coxa as illustrated in *Panorpa venosa* (Plate XXXII, 76) — in which the pleural suture is continuous throughout the length of this first segment of the leg, dividing it into the true coxa (cx^2) and the meron (me^2), terms used by Walton (1900) — is to be recognized only in a few of the lowest families of flies, as the Tipulidae (Plate IX, 2 and 3) and the Rhyphidae (Plate X, 4). In the last two figures evidence is given of the migration of the meron dorsad to become fused eventually with the lower pleural sclerite, the hypoepimeron. In all the higher families of flies this interpretation is placed on the fate of the meron, and the combined meron and hypoepimeron is termed, after Crampton (1914 b), the *meropleurite* (mep^2).

The basalare and subalare sclerites are often present in this order and are figured herein, although not labeled in most of the drawings.

The sternum

To the writer's mind it seems doubtful whether the term *sternopleurite* should be used as its author intended, that is, to refer to a combined sternal and pleural sclerite, or rather to the part of the pleurite which borders on the sternum. The study of the venter of flies is carried on with difficulty because of the proximity of the bases of the legs. But a number of the broader representatives of the group show the same arrangement of sclerites as does *Olfersia americana* (Plate XXXII, 75), in which the two pleurites termed *sternopleurites* meet each other on the ventral side, apparently crowding out the anterior part of the sternum — the *basisternite* (bs) of Crampton (1909). The furcasternite (fs) alone seems to remain in this group.

The metathorax

The tergum

Compared with those of the mesothorax, all three plates of the metathorax are very small. As has been suggested, the large development of

the mesothorax to take care of the powerful wing muscles seems to have taken place at the expense of the following thoracic segment. Especially is this evident in the tergal region, which usually consists of a narrow band of integument connecting the two halteres and providing a single lamella cephalad as its share in the formation of the mesothoracic postscutellar phragma (phg^2_p). It is impossible to make out the four principal subdivisions of the tergum in the metathorax of Diptera. This plate reaches its greatest development in *Psychoda slossoni* (Plate X, 6), so far as the writer's studies have gone. It may be continuous with the epimeron of this segment, as in *Plecia heteroptera* (Plate XIII, 15), *Scenopinus fenestralis* (Plate XVII, 26), *Leptogaster loewi* (Plate XVIII, 28), and many other species, or there may be a suture separating these two sclerites, as in *Anthrax alternata* (Plate XVI, 24), *Platypeza velutina* (Plate XIX, 33), *Macrorchis ausoba* (Plate XXII, 42), and many others; but practically in every case the tergum is separated from the episternum in this segment by the pleural suture.

The pleuron

Although comparatively small sclerites, the episternum (es^3) and the epimeron (em^3) are separated in the metathorax, as in the mesothorax, by the pleural suture. This infolding of the body wall is fairly constant in its extent from the coxae to the base of the halteres, and, studied from the inside, affords one of the best landmarks for homologizing these sclerites. Occasionally in the more generalized species the presence of secondary sutures in the episternal sclerite makes necessary the use of the terms *anepisternum* (aes^3) and *katepisternum* (kes^3), as in *Pachyrrhina ferruginea* (Plate IX, 3) and *Leia winthemi* (Plate XII, 12). Secondary sutures are present also in the posterior pleural sclerite, as in *Dixa modesta* (Plate X, 5) and *Culex canadensis* (Plate XI, 9), but because of the uncertainty as to the line of demarcation between the postscutellum and the epimeron the single term *epimeron* (em^3) is used here.

A large number of peculiarities or variations in the shape of the pleural sclerites are to be found in the various families of this order. Chief among these might be mentioned the following. Commonest of all, perhaps, is a greatly developed episternum with a resulting small epimeron, often nothing more than a narrow strip of chitin and in some cases resulting in the lower part of the epimeron becoming membranous throughout.

Examples of such a development are found in Plates IX, 2, X, 4, 5, and 6, XI, 7, XII, 12, XIII, 13, 14, and 15, XIV, 18, XVII, 27, and XIX, 32. On the other hand, there are examples of the opposite development, the epimeron becoming greatly enlarged at the expense of the episternum, as in *Dolichopus cuprinus* (Plate XVIII, 29).

Another common peculiarity in the epimeral region is the failure of the hypodermal cells of the ventral part of this area to lay down chitin in the integument, with the resulting appearance of the epimeron's moving dorsad (Plates X, 6, XI, 7, XIII, 14, XIV, 16, 17, and 18, XIX, 32, XX, 34 and 35, XXVI, 57, XXVII, 62, XXIX, 67). Many examples of very weak chitin in this lower epimeral sclerite are to be seen. In fact, it is often difficult to say where the epimeron leaves off and the intersegmental abdominal membrane begins (Plates XIII, 13, XXI, 38 and 39, XXII, 41, XXX, 70 and 71, XXXI, 72).

An interesting variation in the lower Nemocera, and one that is very difficult of interpretation, is the movement cephalad of the episternum (es^3) into the mesothorax, with a resulting crowding of the compound sclerite mep^2 into a very small area above the mesothoracic coxa (Plates X, 5 and 6, XI, 9, XII, 10 and 11).

The movement forward of both pairs of legs has caused a decided prolongation of both the episternum (es^3) and the epimeron (em^3) in *Leptogaster loewi* (Plate XVIII, 28) and in *Gastrophilus intestinalis* (Plate XXI, 37); while the prolongation of the coxae in *Leia winthemi* (Plate XII, 12) apparently results in the movement of the episternum (es^3) and the epimeron (em^3) down on the base of the legs.

Sutures sometimes become vestigial, as in the case of *Oncodes incultus* (Plate XVI, 23) in which the pleural suture shows no implex nor scarcely any external evidence of having once existed just above the base of the coxa. The suture between the lower epimeron of the mesothorax and the metathoracic episternum is lacking in *Dixa modesta* (Plate X, 5) and in *Phora concinna* (Plate XIX, 32).

What seemed to be sense pits were found on a number of species, on either the tergum or the pleuron of the metathorax or the basic segments of the abdomen. In a number of cases these have been figured, as in *Thereva fucata* (Plate XVII, 25, em^3 and 2s), in *Leptogaster loewi* (Plate XVIII, 28, t^3), in *Chrysopila ornata* (Plate XV, 21, 2t), and in *Hirmoneura* sp. (Plate XVI, 22, 2t and 2s).

The course of the metathoracic apodeme (Plate XI, 8, ap^3), together with the locations of the metathoracic spiracles (sp^3) and the first abdominal spiracle (1sp), has been a great aid in deciding on these relationships.

Besides the episternum and the epimeron, there is a third pleural sclerite in the metathorax of Diptera which seems to correspond to Crampton's (1914 b) compound sclerite, the pleurotrochantin (fig. 21, ptn.) This compound sclerite is described as being composed of the antecoxale (ac) — which is a narrow marginal strip of the basisternite — the trochantinelle (tnl), the trochantin (tn), and the lower part of the episternum. This sclerite is present in a large number of the higher Diptera, and especially is well marked in the acalyptrate muscids, as *Leria serrata* (Plate XXV, 56, ptn^3), *Rivellia viridulans* (Plate XXVII, 60, ptn^3), and *Sphyracephala brevicornis* (Plate XXIX, 67, ptn^3).

The sternum

As in the mesothorax, the furcasternite — the sternal region which bears the internal diapophyses, or furcae (Plate IX, 1, $apys^3$) — seems to be the only sternite remaining in the order. A glance at the ventral view of *Olfersia americana* (Plate XXXII, 75) will show the marginal lips of the two sclerites termed *pleurotrochantin* (ptn^3) meeting in the mid-ventral line but separating caudad to form the furcasternite (fs^3).

The legs

In no case was the metathoracic coxa found divided by a suture into the true coxa and the meron. If muscular tension causes the ridges of the body wall to be drawn inward for the formation of phragmas, apodemes, and apophyses, this may give a partial explanation of the disappearance of a suture dividing the coxa into two subdivisions, as the metathoracic muscles are greatly reduced in size due to the replacement of the wings by the halteres.

Nothing further need be said concerning the metathoracic legs, except that the coxae show the greatest variation. *Leia winthemi* (Plate XII, 12, cx^3) and *Sciara ochrolabis* (Plate XIII, 13, cx^3) show a considerably elongated condition. In *Blepharocera tenuipes* (Plate XIV, 17, cx^3) the coxae assume a diagonal position between the thorax and the trochanter, while innumerable variations in shape exist. A number of the Acalyptratae show this part of the leg fairly well sculptured with secondary external sutures,

as in *Scatophaga stercoraria* (Plate XXV, 54, cx^3), *Dictya umbrarum* (Plate XXVI, 58, cx^3), and *Sapromyza lupulina* (Plate XXVI, 59, cx^3).

The abdomen

General description

In taking up the discussion of the morphology of the abdomen in its relation to the thorax, the tergites, the sternites, and the spiracles are considered separately. There is little to be said in regard to the pleura aside from the fact that they are commonly taken as the membranous areas between chitinized tergites and sternites. Needless to say, this region shows a considerable variation in width in species showing some deposition of chitin in the sternites and the tergites. A comparison of *Calobata albiceps* (Plate XXVIII, 63) with one of the calyptrate muscids, as *Thelaira nigripes* (Plate XXI, 39), will at once show a wide difference. In the latter example the pleura consist only of narrow inflexed areas between the greatly enlarged tergites and the small sternites which they have overgrown. In the case of species showing no deposition of chitin in the sternal region, as *Phora concinna* (Plate XIX, 32) and *Chlorops* sp. (Plate XXX, 69), and in species showing no deposition of chitin in either the tergal or the sternal region, as *Orphnephila americana* (Plate XIV, 18), *Melophagus ovinus* (Plate XXXI, 73), and *Olfersia americana* (Plate XXXI, 74), it is impossible to speak of a definitive pleuron.

In homologizing the sclerites in the abdomen of Diptera the position of the spiracles is of invaluable aid. In fact, it would be next to impossible to be sure of the sclerites of the first segment without the location of the first abdominal spiracle. An internal study is often necessary to establish the position of this opening to the tracheal system.

In this order, usually five more or less definite abdominal segments may be seen. Beyond the fifth the segments are variously modified to form the genitalia. For this reason it is very easy to overlook spiracles beyond the fifth, as these are often small and show a tendency toward cephalization. It is not unusual to find those of successive segments crowded close together in the same segment in this region.

The tergites

There are many interesting features in the structure of the abdominal tergites. In looking at the group as a whole, it is quite evident that there is a tendency for the first tergite, as well as for the first sternite,

to decrease in relative size. This one is usually nothing more than a narrow band as compared with those that follow. (Plates IX, 2 and 3, X, 4, XIV, 17, XVI, 22, XVII, 26, XVIII, 28 and 30, XX, 35.) Nor can all of this decrease be attributed to the failure of the hypodermal cells to deposit chitin in the membrane just cephalad of the first tergite. It seems very probable that the belief that one segment may gradually disappear owing to the great development of a contiguous segment, is sometimes warranted.

This theory of growth of one segment at the expense of an adjoining one might at first seem to be very good evidence for use in determining what has happened in case of species which show but one chitinized tergite to two spiracles, such as *Lonchoptera* sp. (Plate XIX, 31, 1t and 2t), *Macrorchis ausoba* (Plate XXII, 42, 1t and 2t), *Euaresta festiva* (Plate XXVII, 62, 1t and 2t), *Calobata albiceps* (Plate XXVIII, 63, 1t and 2t), *Sepsis violacea* (Plate XXVIII, 64, 1t and 2t), *Piophila casei* (Plate XXVIII, 65, 1t and 2t), and *Sphyracephala brevicornis* (Plate XXIX, 67, 1t and 2t). But on considering the large number of examples that might be regarded as transitional stages between the well-defined first and second tergite, on the one hand, and the single tergite to represent both, on the other hand, it is easier to believe in a fused condition of these two tergites than in the alternative which would permit the second, or larger, tergite to crowd out the first, or smaller, one altogether. These transitory stages may be seen in a number of species. In *Platypeza velutina* (Plate XIX, 33) there appear two notches in the latero-ventral margin of the tergites at about the place where one would expect to find a dividing suture, and only a lighter band can be seen extending up through the middle of the tergites. In *Pipunculus atlanticus* (Plate XX, 34) the only remaining sign of a suture is a very faint impressed line. In *Tachina mella* (Plate XXI, 38), only a lighter-colored band marks what may have been the position of a suture in its progenitors. This is likewise the case in *Sarcophaga communis* (Plate XXII, 40). Very faint impressed lines exist in *Thelaira nigripes* (Plate XXI, 39), in *Muscina stabulans* (Plate XXII, 41), and in *Dictya umbrarum* (Plate XXVI, 58). Latero-ventral incisions, sometimes with and sometimes without vestigial sutures, are to be seen in some species, as *Sapromyza lupulina* (Plate XXVI, 59), *Parydra limpidipennis* (Plate XXIX, 68), *Chlorops* sp. (Plate XXX, 69), and *Drosophila melanogaster* (*?*) (Plate XXX, 70). A vestigial suture exists in *Rivellia viridulans* (Plate XXVII, 60), while only a bit of membrane is to be found in such

species as *Borborus equinus* (Plate XXVI, 57), *Rhopalomera flaviceps* (Plate XXVII, 61), and *Loxocera pleuritica* (Plate XXIX, 66). These and other examples that might be cited seem to warrant the consideration of this first definitive tergite as the fused first and second tergites. In unbleached specimens these indications of a suture would hardly be noticed, and so it is not to be wondered at that systematists of the order do not always agree as to the number of abdominal segments.

Another possible source of confusion to the systematist is to be found in the division of tergites into secondary parts, either by sutures or a strip of membrane. This may occur in either the first or the second segment. As an example of a tergite being divided into two subdivisions by a suture, one need only refer to the drawings of *Simulium hirtipes* (Plate XIV, 16, $1t_a$ and $1t_p$) and *Midas clavatus* (Plate XVII, 27, $1t_a$ and $1t_p$). Examples of division by membrane may be seen in *Sciara ochrolabis* (Plate XIII, 13, $1t_a$ and $1t_p$) and in *Plecia heteroptera* (Plate XIII, 15, $2t_a$ and $2t_p$). An example of the separation of the first and second tergites by a narrow band of membrane or weak chitin is given in *Allognosta fuscitarsis* (Plate XV, 19).

In several species the first abdominal tergite has so overgrown the thorax that on superficial examination it appears as a part of this region. This condition is most evident in such species as *Chrysops indus* (Plate XV, 20, 1t) and *Anthrax alternata* (Plate XVI, 24, 1t).

A very noticeable character, and one that was first found in *Myopa vesiculosa* (Plate XX, 36), is an adventitious suture arising from the latero-cephalic margin of the first abdominal tergite and running caudo-dorsad through this tergite often to the cephalic margin of the second tergite. This varies considerably in its degree of development in different species, but was found in all the species examined among both the Calyptratae and the Acalyptratae. Generally speaking, this suture is less highly developed in the calyptrate than in the acalyptrate muscids, as is seen on comparing *Thelaira nigripes* (Plate XXI, 39) and *Muscina stabulans* (Plate XXII, 41) with *Scatophaga stercoraria* (Plate XXV, 54) and *Sepsis violacea* (Plate XXVIII, 64).

The sternites

The greater demand made upon the tergites for the attachment of muscles than upon the sternites is clearly reflected in the larger number

of species found in which the sternites were composed of membrane or very weak chitin. In so far as the tergites are concerned, these are of such a composition only in *Orphnephila americana* (Plate XIV, 18); while the following species show this condition in so far as the sternites are concerned: *Simulium hirtipes* (Plate XIV, 16), *Orphnephila americana* (Plate XIV, 18), *Phora concinna* (Plate XIX, 32), *Gastrophilus intestinalis* (Plate XXI, 37), *Chlorops* sp. (Plate XXX, 69), *Melophagus ovinus* (Plate XXXI, 73), and *Olfersia americana* (Plate XXXI, 74). Instances of the first abdominal tergite remaining membranous, possibly to facilitate the movement of the caudal end of the abdomen, are not uncommon. This is the case in *Anopheles quadrimaculata* (Plate XII, 10), *Midas clavatus* (Plate XVII, 27), *Lonchoptera* sp. (Plate XIX, 31), *Pipunculus atlanticus* (Plate XX, 34), and *Borborus equinus* (Plate XXVI, 57). Other species, such as *Rhabdophaga strobiloides* (Plate XIII, 14) and *Drosophila melanogaster* (*?*) (Plate XXX, 70), have a slight amount of chitin laid down in this sternite.

The same forces that have had their effect in decreasing the size of the first abdominal tergites have produced the same result in the sternites of a larger number of species. Most decidedly is this the case in *Trichocera brumalis* (Plate X, 4, 1s), in *Thereva fucata* (Plate XVII, 25, 1s), in *Scenopinus fenestralis* (Plate XVII, 26, 1s), in *Leptogaster loewi* (Plate XVIII, 28, 1s), in *Dolichopus cuprinus* (Plate XVIII, 29, 1s), and in *Muscina stabulans* (Plate XXII, 41, 1s); while the same condition holds to a lesser extent in *Leia winthemi* (Plate XII, 12, 1s), in *Sciara ochrolabis* (Plate XIII, 13, 1s), in *Hirmoneura* sp. (Plate XVI, 22, 1s), and in *Sarcophaga communis* (Plate XXII, 40, 1s).

Subdivisions of primary sternites are found oftener than are subdivisions of primary tergites, the second sternite being the one oftenest modified in this way. In *Pachyrrhina ferruginea* (Plate IX, 3, $1s_a$ and $1s_p$), in *Plecia heteroptera* (Plate XIII, 15, $2s_a$ and $2s_p$), in *Rhamphomyia* sp. (Plate XVIII, 30, $2s_a$ and $2s_p$), and in *Calobata albiceps* (Plate XXVIII, 63, $2s_a$ and $2s_p$), the anterior part is separated from the posterior part of the second sternite by membrane.

In only one species, *Chrysops indus* (Plate XV, 20, 1s and 2s), were the first and second sternites found to have coalesced. Here a double row of sense pits marks the usual position of the suture between the first and the second segment.

The spiracles

The number of abdominal spiracles in Diptera varies from five to eight, with seven as the number oftenest met with. Data on this point are given in the list of species on pages 258 to 261. A glance at these data will show these openings to the tracheal system appearing either in membrane or in chitin, but oftener in membrane, as would be expected when it is considered that the normal position of the row of abdominal spiracles may be assumed to be midway between dorsum and venter in the latus. In a large majority of families this region remains membranous, and only in relatively few have the so-called tergites usurped the pleural region enough to include the spiracles. It amounts to this: when the hypodermal cells in the pleural region have become stimulated enough to deposit chitin, then, in the order Diptera, this region forfeits its right to be known as a part of the pleuron and must be called a part of the tergum. This arrangement of spiracles in the order certainly goes to show that if for any reason there is need for rigidity in a certain region, it is no more difficult to lay down chitin around spiracles than at any other place.

As a rule it may be said that the abdominal spiracles of species of the Nemocera and Brachycera groups in the suborder Orthorrhapha are to be found in membrane. But immediately the outstanding exceptions, in so far as the writer's study has gone, would have to be mentioned in *Oncodes incultus* (Plate XVI, 23) and in *Lonchoptera* sp. (Plate XIX, 31). In the suborder Cyclorrhapha, the representative families of the Athericera and the Acalyptratae tend to permit their abdominal spiracles to remain in membrane. A number of exceptions would have to be raised here, however, such as *Platypeza velutina* (Plate XIX, 33), *Parydra limpidipennis* (Plate XXIX, 68), and others. Among the families of the Calyptratae of this suborder, the tendency is toward the deposition of chitin about these spiracular openings because of the excessive downward extension of the tergites. It is needless to say that this is not the case in all species of every family in the group. A glance at the record of the species of anthomyids studied will expel any doubts concerning this last statement.

In most of the Diptera, and especially in the more generalized species, the first abdominal spiracle is to be found in the anterior part of the segment and very often in the membrane between the metathorax and the first abdominal segment. The usual position of the remaining spiracles is

near the middle of the segment, if anything slightly cephalad from the center. Such an arrangement as that in *Oncodes incultus* (Plate XVI, 23), in which the first abdominal spiracle appears in the posterior part of the segment, is very unusual, while examples of the shifting of all spiracles to the anterior end, as in *Allognosta fuscitarsis* (Plate XV, 19), is not at all uncommon.

SPECIES OF ANTHOMYIDS

Because of the uncertain systematic position of some genera within the family Anthomyiidae, species of twelve genera of this family were studied and figured (Plates XXII, 42, XXIII, and XXIV, inclusive). Considerable uniformity is shown in the structure of the region around the base of the abdomen. In each case were the episternum (es^3) and the epimeron (em^3), as well as the pleurotrochantin (ptn^3), of the metathorax clearly defined. The fused condition of the first and second abdominal tergites, in contrast to the separate state of the corresponding sternites, held in each. Also, the adventitious suture of the first abdominal tergite was constant. The greatest variation found in these species, perhaps, was in the location of the abdominal spiracles. This can be seen by referring to the information concerning abdominal spiracles which accompanies each species in the list on pages 258 to 261.

SUMMARY[2]

Points brought out in a summary of an investigation of this nature must of necessity be based upon a study of a rather limited amount of material, considering the number of genera and species in the entire order. However, uniformities existing in single species of so wide a range of families as the writer has been permitted to examine, will at least suggest points to be tested in a wider range of species within certain families. Furthermore, they cannot help adding their bit in the task of unraveling the phylogeny of the order Diptera.

One of the most interesting characteristics to appear in a large number of families is what has been termed an adventitious suture, or a suture running caudo-dorsad from the anterior margin of the first abdominal tergite and one not to be confused with the suture dividing the first and the second tergite although the two are closely related to each other.

[2]The chart from which this summary was deducted is inserted at the end of this paper.

This suture was found in species of all the families studied among the Calyptratae and the Acalyptratae, but in only one family outside of these two groups, in *Myopa vesiculosa* (Plate XX, 36) of the family Conopidae.

Closely associated with the appearance of this suture is a tendency toward the coalescence of the first two abdominal tergites. This tendency toward fusion occurs in all the families of the Acalyptratae with the exception of the Scatophagidae (Plate XXV, 54), the Heteroneuridae (Plate XXV, 55), and the Helomyzidae (Plate XXV, 56); and in all the families of the Calyptratae with the exception of the Oestridae (Plate XXI, 37). Aside from the families of these two groups it occurs only in the Conopidae (Plate XX, 36), the Pipunculidae (Plate XX, 34), the Platypezidae (Plate XIX, 33), and the Lonchopteridae (Plate XIX, 31). But at least five different stages in the development of this tendency can be pointed out if there are included the families showing both the adventitious suture and a complete suture between the first and second tergites, as the Oestridae (Plate XXI, 37), the Scatophagidae (Plate XXV, 54), the Heteroneuridae (Plate XXV, 55), and the Helomyzidae (Plate XXV, 56). The adventitious suture and only the dorsal part of the suture dividing the two tergites are found in the Conopidae (Plate XX, 36), the Sarcophagidae (Plate XXII, 40), the Sciomyzidae (Plate XXVI, 58), the Piophilidae (Plate XXVIII, 65), and the Geomyzidae (Plate XXX, 71). Further, the adventitious suture and only the ventral part of the suture dividing the first and second tergites are found in the Borboridae (Plate XXVI, 57), the Sapromyzidae (Plate XXVI, 59), the Ortalidae (Plate XXVII, 60), the Sepsidae (Plate XXVIII, 64), the Ephydridae (Plate XXIX, 68), the Oscinidae (Plate XXX, 69), and the Drosophilidae (Plate XXX, 70). The next stage would be represented by families showing the adventitious suture alone, in a few cases the suture between the tergites being represented by a semblance of membrane, as in the Tachinidae (Plate XXI, 38), the Dexiidae (Plate XXI, 39), the Muscidae (Plate XXII, 41), the Anthomyiidae (Plate XXII, 42), the Rhopalomeridae (Plate XXVII, 61), the Trypetidae (Plate XXVII, 62), the Micropezidae (Plate XXVIII, 63), the Psilidae (Plate XXIX, 66), the Diopsidae (Plate XXIX, 67), and the Agromyzidae (Plate XXXI, 72). Finally, in some families no marked evidence of either suture was to be found, as in the Lonchopteridae (Plate XIX, 31), the Platypezidae (Plate XIX, 33), and the Pipunculidae (Plate XX, 34). Among the species of anthomyids

studied, two of these stages were represented, eight species showing the adventitious suture and the ventral part of the suture separating the first and second tergites, and four species showing only the adventitious suture.

In drawing conclusions regarding any uniformities existing among Diptera in respect to the location of abdominal spiracles, perhaps it would be best to disregard the first and those beyond the fifth segment, and consider only the second, third, fourth, and fifth segments. The integument in which the first abdominal spiracle is located is the most subject to change, as it is just at the point of attachment of the abdomen to the thorax. As there is a necessity for flexibility at this point, the body wall is usually membranous, and as a result the first abdominal spiracle is, with few exceptions, as in the cyrtid (Plate XVI, 23), the lonchopterid (Plate XIX, 31), the tachinid (Plate XXI, 38), the dexiid (Plate XXI, 39), and three species of anthomyids (Plates XXII, 42, and XXIII, 45 and 48), found in membrane. Beyond the fifth segment, the spiracles are so affected by the forces producing the modification of the segments into the genitalia that these too are unreliable. But in considering the second, third, fourth, and fifth spiracles in regard to location in membrane or chitin, some uniformities are seen. All four of these spiracles in each family of the Calyptratae except the Oestridae, in which all are in the membrane, are found in chitin. Among the Acalyptratae, all four spiracles in the Scatophagidae and the Ephydridae, and the third, fourth, and fifth in the Oscinidae, are found in chitin. All other representatives of families have these spiracles in membrane. Aside from these two groups, only scattered cases are found in which these spiracles are surrounded by chitin. In the Cyrtidae, all four are in chitin; in the Lonchopteridae and the Platypezidae, only the third, fourth, and fifth are in chitin.

The pleuro-trochantin (ptn^3) of the metathorax appears as a chitinized sclerite in all the Cyclorrhapha, with the possible exception of the Oestridae (Plate XXI, 37), the Tachinidae (Plate XXI, 38), and the Pipunculidae (Plate XX, 34). Among the Brachycera there seem to be two families showing true chitin in this sclerite, the Asilidae (Plate XVIII, 28) and the Lonchopteridae (Plate XIX, 31). This sclerite appears as membrane or as questionable chitin, if at all, in all other families.

In a few families it was rather difficult to separate the epimeron of the metathorax from the sclerites of the first abdominal segment. These

species sometimes give one the impression that the epimeron of the metathorax is an abdominal sclerite and the first tergite is a thoracic sclerite. Because, for the most part, this confused condition exists among the Brachycera, attention is called to it. This is the case in all the families except the Stratiomyiidae (Plate XV, 19), the Empididae (Plate, XVIII, 30), the Lonchopteridae (Plate XIX, 31), and the Phoridae (Plate XIX, 32).

Perhaps one of the clearest characters that nature has supplied in the area studied, and one on which the whole group of flies can be divided, is the pleural suture of the mesothorax. In the Nemocera with the exception of the Psychodidae, and in the Brachycera with the exception of the Cyrtidae, this suture runs more or less straight from the coxa to the wing process. If it bends forward at all it is on a rather easy curve, but in all the Brachycera of the Orthorrhapha, with the exception of the one cited above, and in all the Cyclorrhapha, this suture takes an abrupt turn cephalad (in some cases the angle is equal to 90° or more) in its course from the leg to the wing area.

Lastly, the writer wishes to call attention to the presence of a tongue-like structure in the membrane of the mesothoracic coxae of all the Calyptratae and the Acalyptratae, with the exception of the Oestridae, and its absence in all other families except the Syrphidae.

These characteristics do not as a whole point to the same places for the division of the order as the one adopted in this paper, or to any other single classification. But there are characters, such as the presence or absence of the adventitious suture and the character of the pleural suture of the mesothorax, which divide rather definitely where they strike and should be of value for that reason. Certainly this investigation has emphasized the fact that the last word has not been said on the systematic position of some members in such families as the Cyrtidae, the Oestridae, the Scatophagidae, the Ephydridae, the Oscinidae, and a number of others whose study has offered obstructions to uniformities within a time-honored system.

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Memoir 39, *The Genetic Relations of Plant Colors in Maize*, the fifth preceding number in this series of publications, was mailed on July 19, 1921.

yptratae

Character Summary Chart

Key
+ Yes — No
? Uncertain

	♀	♂	♀	♀	♂	♀	♀	♂	♀	♀
	Piophila casei	*Loxocera pleuritica*	*Sphyracephala brevicornis*	*Parydra limpidipennis*	*Chlorops* sp.	*Drosophila melanogaster*(?)	*Anthomyza gracilis*	*Agromyza lateralis*	*Melophagus ovinus*	*Olfersia americana*
	Piophilidae	Psilidae	Diopsidae	Ephydridae	Oscinidae	Drosophilidae	Geomyzidae	Agromyzidae	Hippoboscidae	Hippoboscidae
Mesothoracic pleural suture makir forward in its course from coxa	+	+	+	+	+	+	+	+		+
Tongue-like structure present mesothoracic coxa (cx^2)	+	+	+	+	+	+	?	+	?	?
Metathoracic pleurotrochantin (chitinized sclerite	+	+	+	+	+	+	+	+	?	+
Thoracic and abdominal scleri entiated	+	+	+	+	+	+	+	+	+	+
Adventitious suture present i tergite	+	+	+	+	+	+	+	+	+	+
Suture between first and second present entire	—	—	—	—	—	—	—	—	—	—
First abdominal tergite subdivi branous (m)	—	—	—	—	—	—	—	—	—	—
Second abdominal tergite subdi branous (m)	—	—	—	—	—	—	—	—	—	—
First abdominal sternite subdiv branous (m)	—	—	—	—	m	m	—	—	m	m
Second abdominal sternite subd branous (m)	—	—	—	—	m	—	—	—	m	m
First abdominal spiracle in mem	+	+	+	+	+	+	+	+	+	+
Second abdominal spiracle in m	+	+	+	—	+	+	+	+	+	+
Third abdominal spiracle in me	+	+	+	—	—	+	+	+	+	+
Fourth abdominal spiracle in m	+	+	+	—	—	+	+	+	+	+
Fifth abdominal spiracle in me	+	+	+	—	—	+	+	+	+	+
Number of abdominal spiracles	7	7	7	6	6	7	6 or 7	7	7	7

ix.
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Character Summary Chart

Key
+ Yes — No
? Uncertain

Orthorrhapha — Nemocera — Brachycera — Athericera — Calyptratae — Cyclorrhapha — Acalyptratae

Species	Pedicia albivitta	Pachyrrhina ferruginea	Trichocera brumalis	Dixa modesta	Psychoda slossoni	Chironomus ferrugineovitta	Culex canadensis	Anopheles quadrimaculata	Corethra albipes	Leia winthemi	Sciara ochrolabis	Rhabdophaga strobiloides
Sex Group o[f]	♀	♂	♀	♀	♀	♂	♂	♀	♀	♀	♂	♂
Family	Tipulidae	Tipulidae	Rhyphidae	Dixidae	Psychodidae	Chironomidae	Culicidae	Culicidae	Culicidae	Mycetophilidae	Sciaridae	Cecidomyiidae
…esothoracic pleural suture making an abrupt bend forward in its course from coxa to wing process	—	—	—	—	+	—	—	—	—	—	—	—
…ongue-like structure present in membrane of mesothoracic coxa (cx^2)	—	—	—	—	—	—	—	—	—	—	—	—
…etathoracic pleurotrochantin (ptn^3) present as a chitinized sclerite	?	—	?	—	—	—	—	—	—	—	—	—
…oracic and abdominal sclerites clearly differentiated	+	+	+	+	—	+	+	+	+	+	+	+
…ventitious suture present in first abdominal tergite	—	—	—	—	—	—	—	—	—	—	—	—
…ure between first and second abdominal tergites present entire	+	+	+	+	+	+	+	+	+	+	+	+
…st abdominal tergite subdivided (s) or membranous (m)	—	—	—	—	—	—	—	—	—	—	s	—
…ond abdominal tergite subdivided (s) or membranous (m)	—		—	—	—	—	—	—	—	—	—	—
…t abdominal sternite subdivided (s) or membranous (m)	—	s	—	—	—	—	—	m	—	—	—	—
…nd abdominal sternite subdivided (s) or membranous (m)	s	—	—	—	—	—	—	—	—	—	—	—
…t abdominal spiracle in membrane	+	+	+	+	+	+	+	+	+	+	+	+
…nd abdominal spiracle in membrane	+	+	+	+	+	+	+	+	+	+	+	+
…d abdominal spiracle in membrane	+	+	+	+	+	+	+	+	+	+	+	+
…th abdominal spiracle in membrane	+	+	+	+	+	+	+	+	+	+	+	+
…abdominal spiracle in membrane	+	+	+	+	+	+	+	+	+	+	+	+
…ber of abdominal spiracles	8	7	7	7	7	7 or 8	7	7	7	7	7	7

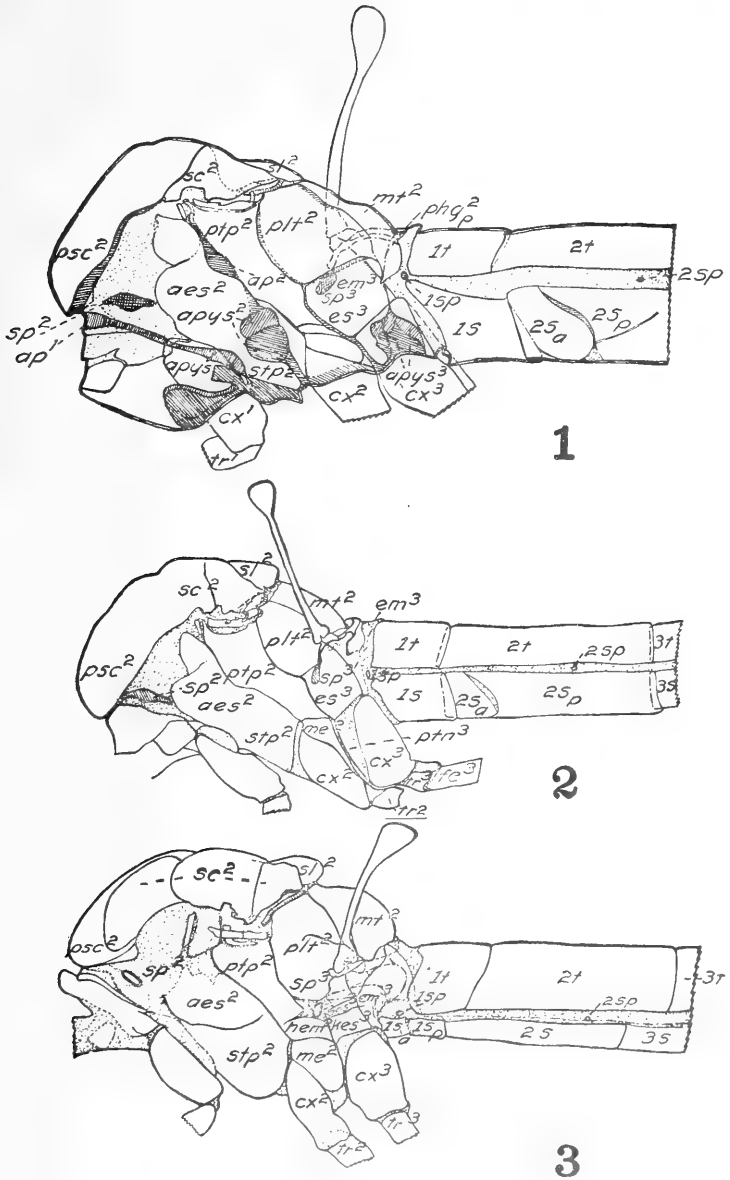
Species	Plecia heteroptera	Simulium hirtipes	Blepharocera tenuipes	Orphnephila americana	Allognosta fuscitarsis	Chrysops indus	Chrysopila ornata	Hirmoneura sp.	Oncodes incultus	Anthrax alternata	Thereva fucata	Scenopinus fenestralis
Sex Group o[f]	♀	♂	♀	♀	♀	♂	♂	♀	♀	♀	♂	♀
Family	Bibionidae	Simuliidae	Blepharoceridae	Orphnephilidae	Stratiomyiidae	Tabanidae	Leptidae	Nemistrinidae	Cyrtidae	Bombyliidae	Therevidae	Scenopinidae
…esothoracic pleural suture making an abrupt bend forward in its course from coxa to wing process	—	—	—	—	+	+	+	+	—	+	+	+
…ongue-like structure present in membrane of mesothoracic coxa (cx^2)	—	—	—	—	—	—	—	—	—	—	—	—
…etathoracic pleurotrochantin (ptn^3) present as a chitinized sclerite	?	—	—	—	—	—	—	?	—	—	?	—
…oracic and abdominal sclerites clearly differentiated	+	—	+	+	+	—	—	—	—	—	—	—
…ventitious suture present in first abdominal tergite	—	—	—	—	—	—	—	—	—	—	—	—
…ure between first and second abdominal tergites present entire	+	+	+	+	+	+	+	+	+	+	+	+
…st abdominal tergite subdivided (s) or membranous (m)	—	s	—	m	—	—	—	—	—	—	—	—
…ond abdominal tergite subdivided (s) or membranous (m)	s	—	—	m	—	—	—	—	—	—	—	—
…t abdominal sternite subdivided (s) or membranous (m)	—	m	—	m	—	Coalesced	—	—	—	—	—	—
…nd abdominal sternite subdivided (s) or membranous (m)	s	m	—	m	—		s	—	—	—	—	—
…t abdominal spiracle in membrane	+	—	+	+	+	+	+	+	—	+	+	+
…nd abdominal spiracle in membrane	+	+	+	+	+	+	+	+	—	+	+	+
…d abdominal spiracle in membrane	+	+	+	+	+	+	+	+	—	+	+	+
…th abdominal spiracle in membrane	+	+	+	+	+	+	+	+	—	+	+	+
…abdominal spiracle in membrane	+	+	+	+	+	+	+	+	—	+	+	+
…ber of abdominal spiracles	8	7	7	7 or 8	7	7	7	7	6	7	7	7 or 8

Species	Midas clavatus	Leptogaster loewi	Dolichopus cuprinus	Rhamphomyia sp.	Lonchoptera sp.	Phora concinna	Platypeza velutina	Pipunculus atlanticus	Syrphus americanus	Myopa vesiculosa	Gastrophilus intestinalis	Tachina mella
Sex Group o[f]	♀	♀	♂	♀	♀	♀	♀	♀	♂	♂	♀	♀
Family	Midaidae	Asilidae	Dolichopodidae	Empididae	Lonchopteridae	Phoridae	Platypezidae	Pipunculidae	Syrphidae	Conopidae	Oestridae	Tachinidae
…esothoracic pleural suture making an abrupt bend forward in its course from coxa to wing process	+	+	+	+	+	+	+	+	+	+	+	+
…ongue-like structure present in membrane of mesothoracic coxa (cx^2)	—	—	—	—	—	—	—	—	+	—	—	+
…etathoracic pleurotrochantin (ptn^3) present as a chitinized sclerite	?	+	—	—	+	+	+	—	+	+	—	—
…oracic and abdominal sclerites clearly differentiated	—	—	—	+	+	+	+	—	—	+	+	+
…ventitious suture present in first abdominal tergite	—	—	—	—	—	—	—	—	—	+	+	+
…ure between first and second abdominal tergites present entire	+	+	+	+	—	+	—	—	+	—	+	—
…st abdominal tergite subdivided (s) or membranous (m)	s	—	—	—	—	—	—	—	—	—	—	—
…ond abdominal tergite subdivided (s) or membranous (m)	—	—	—	—	—	—	—	—	—	—	—	—
…t abdominal sternite subdivided (s) or membranous (m)	m	—	—	—	m	m	—	m	—	—	m	—
…nd abdominal sternite subdivided (s) or membranous (m)	s	—	—	s	—	m	—	—	—	—	m	—
…t abdominal spiracle in membrane	+	+	+	+	—	+	+	+	+	+	+	—
…nd abdominal spiracle in membrane	+	+	+	+	—	+	—	+	+	+	+	—
…d abdominal spiracle in membrane	+	+	+	+	—	+	—	+	+	+	+	—
…th abdominal spiracle in membrane	+	+	+	+	—	+	—	+	+	+	+	—
…abdominal spiracle in membrane	+	+	+	+	+	+	+	+	+	+	+	—
…ber of abdominal spiracles	8	7 or 8	7	7	7	6 or 7	7	7	7	7	7	7

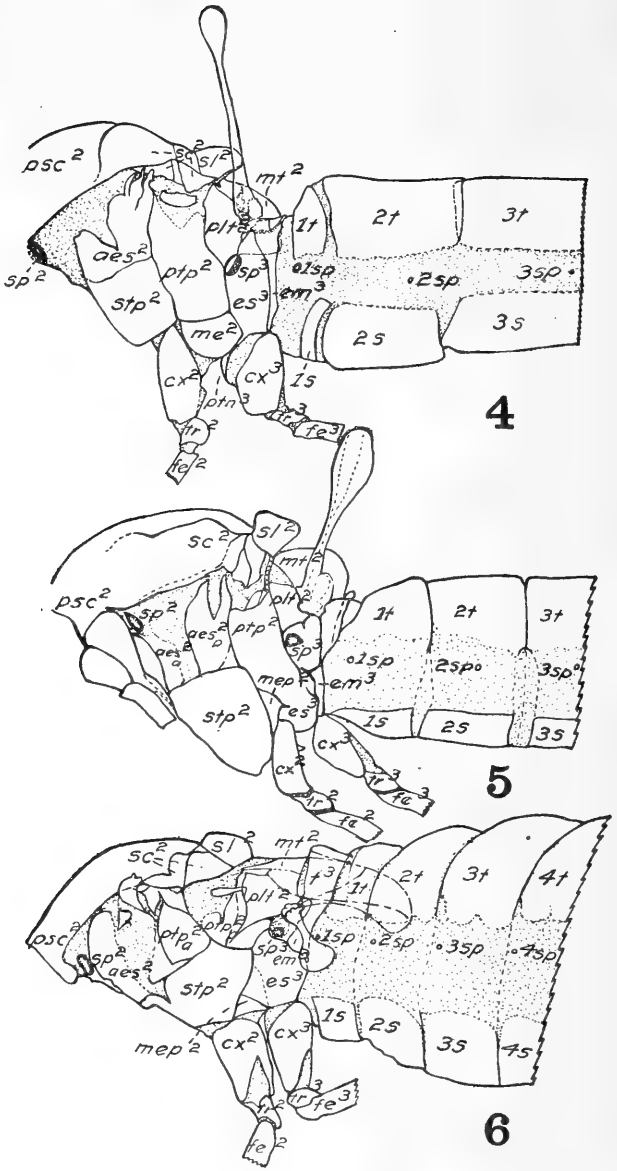
Species	Thelaira nigripes	Sarcophaga communis	Muscina stabulans	Macrorchis ausoba	Chortophila cilicrura	Hylephila paludis	Schoenomyza dorsalis	Ophyra leucostoma	Lispa sociabilis	Limnophora aequifrons	Eremomyia cylindrica	Pegomyia affinis
Sex Group o[f]	♂	♂	♀	♂	♂	♀	♀	♂	♀	♂	♀	♀
Family	Dexiidae	Sarcophagidae	Muscidae	Anthomyiidae	Anthomyiidae	Anthomyiidae	Anthomyiidae	Anthomyiidae	Anthomyiidae	Anthomyiidae	Anthomyiidae	Anthomyiidae
…esothoracic pleural suture making an abrupt bend forward in its course from coxa to wing process	+	+	+	+	+	+	+	+	+	+	+	+
…ongue-like structure present in membrane of mesothoracic coxa (cx^2)	+	+	+	+	+	+	+	+	+	+	+	+
…etathoracic pleurotrochantin (ptn^3) present as a chitinized sclerite	+	+	+	+	+	+	+	+	+	+	+	+
…oracic and abdominal sclerites clearly differentiated	+	+	+	+	+	+	+	+	+	+	+	+
…ventitious suture present in first abdominal tergite	+	+	+	+	+	+	+	+	+	+	+	+
…ure between first and second abdominal tergites present entire	—	—	—	—	—	—	—	—	—	—	—	—
…st abdominal tergite subdivided (s) or membranous (m)	—	—	—	—	—	—	—	—	—	—	—	—
…ond abdominal tergite subdivided (s) or membranous (m)	—	—	—	—	—	—	—	—	—	—	—	—
…t abdominal sternite subdivided (s) or membranous (m)	—	—	—	—	—	—	—	—	—	—	—	—
…nd abdominal sternite subdivided (s) or membranous (m)	—	—	—	—	—	—	—	—	—	—	—	—
…t abdominal spiracle in membrane	—	+	+	—	+	+	—	+	+	—	+	+
…nd abdominal spiracle in membrane	—	—	—	—	—	—	—	—	—	—	—	—
…d abdominal spiracle in membrane	—	—	—	—	—	—	—	—	—	—	—	—
…th abdominal spiracle in membrane	—	—	—	—	—	—	—	—	—	—	—	—
…abdominal spiracle in membrane	—	—	—	—	—	—	—	—	—	—	—	—
…ber of abdominal spiracles	7	7	7	7	7	7	5	7	6	7	7	7

Species	Hylemyia lipsia	Anthomyia radicum	Helecnema umbratica	Scatophaga stercoraria	Clusia lateralis	Leria serrata	Borborus equinus	Dictya umbrarum	Sapromyza lupulina	Rivellia viridulans	Rhopalomera flaviceps	Euaresta festiva
Sex Group o[f]	♀	♂	♀	♂	♀	♂	♀	♀	♂	♀	♀	♀
Family	Anthomyiidae	Anthomyiidae	Anthomyiidae	Scatophagidae	Heteroneuridae	Helomyzidae	Borboridae	Sciomyzidae	Sapromyzidae	Ortalidae	Rhopalomeridae	Trypetidae
…esothoracic pleural suture making an abrupt bend forward in its course from coxa to wing process	+	+	+	+	+	+	+	+	+	+	+	+
…ongue-like structure present in membrane of mesothoracic coxa (cx^2)	+	+	+	+	+	+	+	+	+	+	+	+
…etathoracic pleurotrochantin (ptn^3) present as a chitinized sclerite	+	+	+	+	+	+	+	+	+	+	+	+
…oracic and abdominal sclerites clearly differentiated	+	+	+	+	+	+	+	+	+	+	+	+
…ventitious suture present in first abdominal tergite	+	+	+	+	+	+	+	+	+	+	+	+
…ure between first and second abdominal tergites present entire	—	—	—	+	+	+	—	—	—	—	—	—
…st abdominal tergite subdivided (s) or membranous (m)	—	—	—	—	—	—	—	—	—	—	—	—
…ond abdominal tergite subdivided (s) or membranous (m)	—	—	—	—	—	—	—	—	—	—	—	—
…t abdominal sternite subdivided (s) or membranous (m)	—	—	—	—	—	—	m	—	—	—	—	—
…nd abdominal sternite subdivided (s) or membranous (m)	—	—	—	—	—	—	—	—	—	—	—	—
…t abdominal spiracle in membrane	+	+	+	+	+	+	+	+	+	+	+	+
…nd abdominal spiracle in membrane	—	—	—	—	+	+	+	+	+	+	+	+
…d abdominal spiracle in membrane	—	—	—	—	+	+	+	+	+	+	+	+
…th abdominal spiracle in membrane	—	—	—	—	+	+	+	+	+	+	+	+
…abdominal spiracle in membrane	—	—	—	—	+	+	+	+	+	+	+	+
…ber of abdominal spiracles	7	7	5	7	7	7	7	7	7	7	7	7

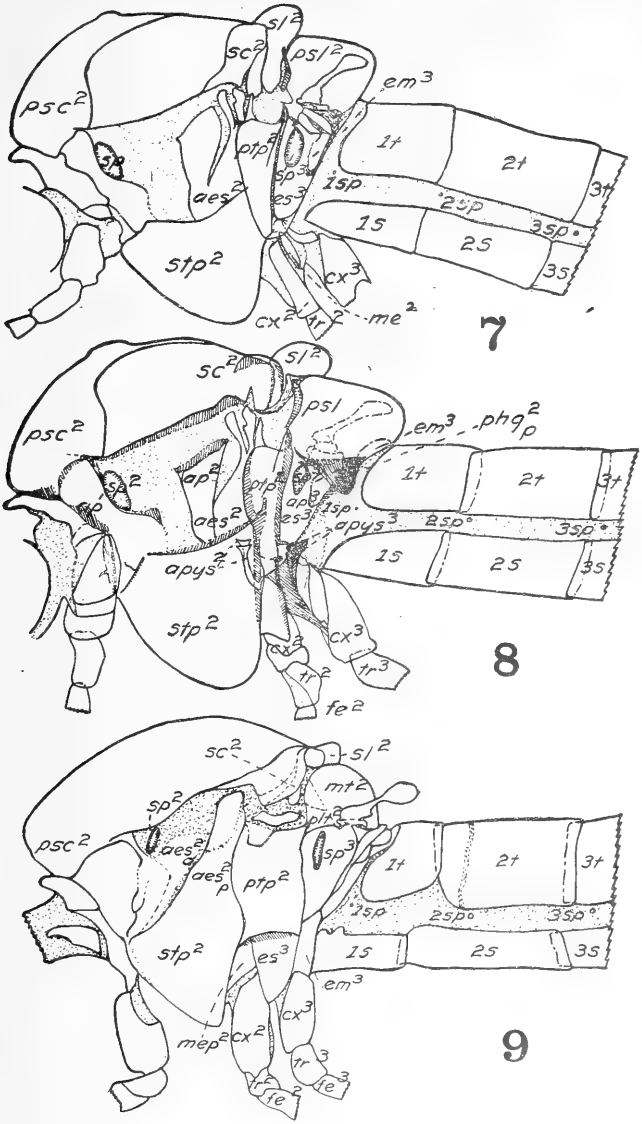
Species	Calobata albiceps	Sepsis violacea	Piophila [illegible]	[illegible]	Sphyracephala [illegible]	Parydra limpidipennis	Chlorops sp.	Drosophila melanogaster(?)	Anthomyza gracilis	Agromyza lateralis	Melophagus ovinus	Olfersia americana
Sex Group o[f]	♀	♀	♀	[illegible]	[illegible]	♀	♂	♀	♀	♂	♀	♀
Family	Micropezidae	Sepsidae	Piophilidae	Psilidae	Diopsidae	Ephydridae	Oscinidae	Drosophilidae	Geomyzidae	Agromyzidae	Hippoboscidae	Hippoboscidae
…esothoracic pleural suture making an abrupt bend forward in its course from coxa to wing process	+	+	+	+	+	+	+	+	+	+		+
…ongue-like structure present in membrane of mesothoracic coxa (cx^2)	+	+	+	+	+	+	+	+	?	+	?	?
…etathoracic pleurotrochantin (ptn^3) present as a chitinized sclerite	+	+	+	+	+	+	+	+	+	+	?	+
…oracic and abdominal sclerites clearly differentiated	+	+	+	+	+	+	+	+	+	+	+	+
…ventitious suture present in first abdominal tergite	+	+	+	+	+	+	+	+	+	+	+	+
…ure between first and second abdominal tergites present entire	—	—	—	—	—	—	—	—	—	—	—	—
…st abdominal tergite subdivided (s) or membranous (m)	—	—	—	—	—	—	—	—	—	—	—	—
…ond abdominal tergite subdivided (s) or membranous (m)	—	—	—	—	—	—	—	—	—	—	—	—
…t abdominal sternite subdivided (s) or membranous (m)	—	—	—	—	—	—	m	m	—	—	m	m
…nd abdominal sternite subdivided (s) or membranous (m)	s	—	—	—	—	—	m	—	—	—	m	m
…t abdominal spiracle in membrane	+	+	+	+	+	+	+	+	+	+	+	+
…nd abdominal spiracle in membrane	+	+	+	+	+	—	+	+	+	+	+	+
…d abdominal spiracle in membrane	+	+	+	+	+	—	—	+	+	+	+	+
…th abdominal spiracle in membrane	+	+	+	+	+	—	—	+	+	+	+	+
…abdominal spiracle in membrane	+	+	+	+	+	—	—	+	+	+	+	+
…ber of abdominal spiracles	7	7	7	7	7	6	6	7	6 or 7	7	7	7



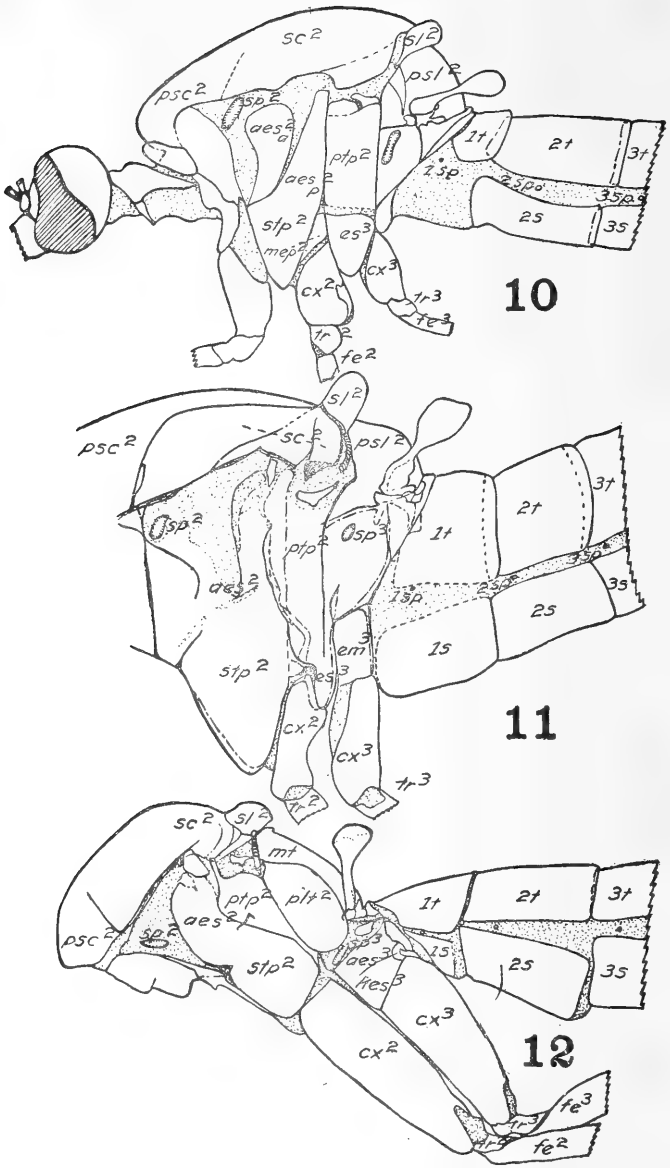
1, *Pedicia albivitta*, female (Tipulidae); internal view, showing endothorax. 2, *Pedicia albivitta*, female (Tipulidae). 3, *Pachyrrhina ferruginea*, male (Tipulidae)



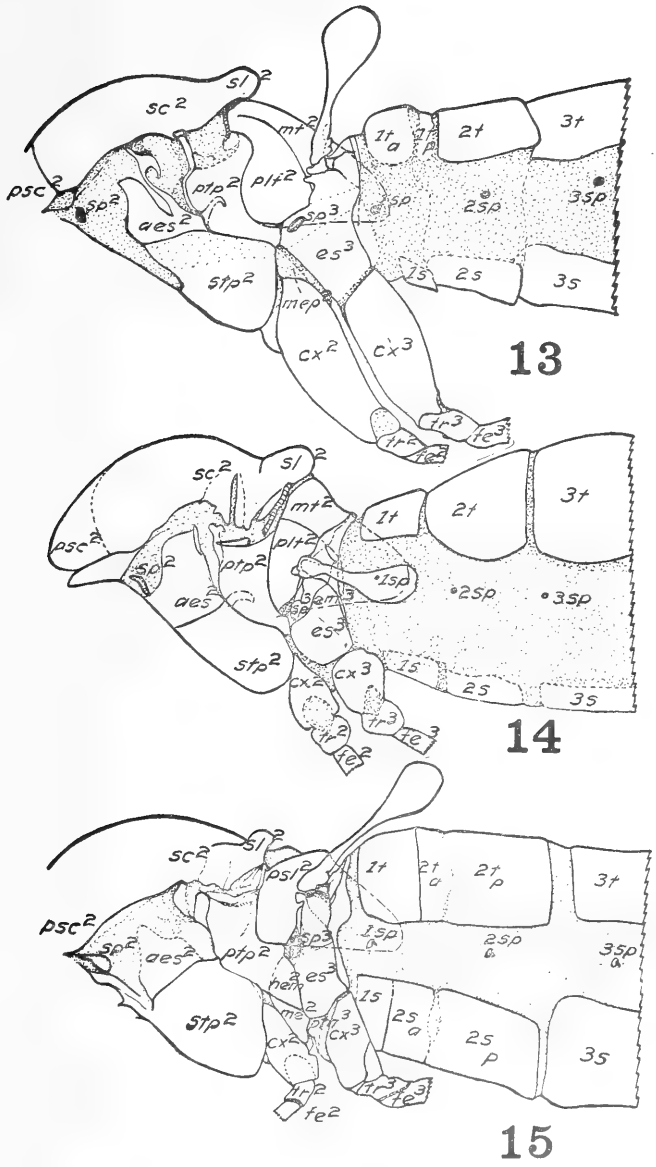
4, *Trichocera brumalis*, female (Rhyphidae). 5, *Dixa modesta*, female (Dixidae). 6, *Psychoda slossoni*, female (Psychodidae)



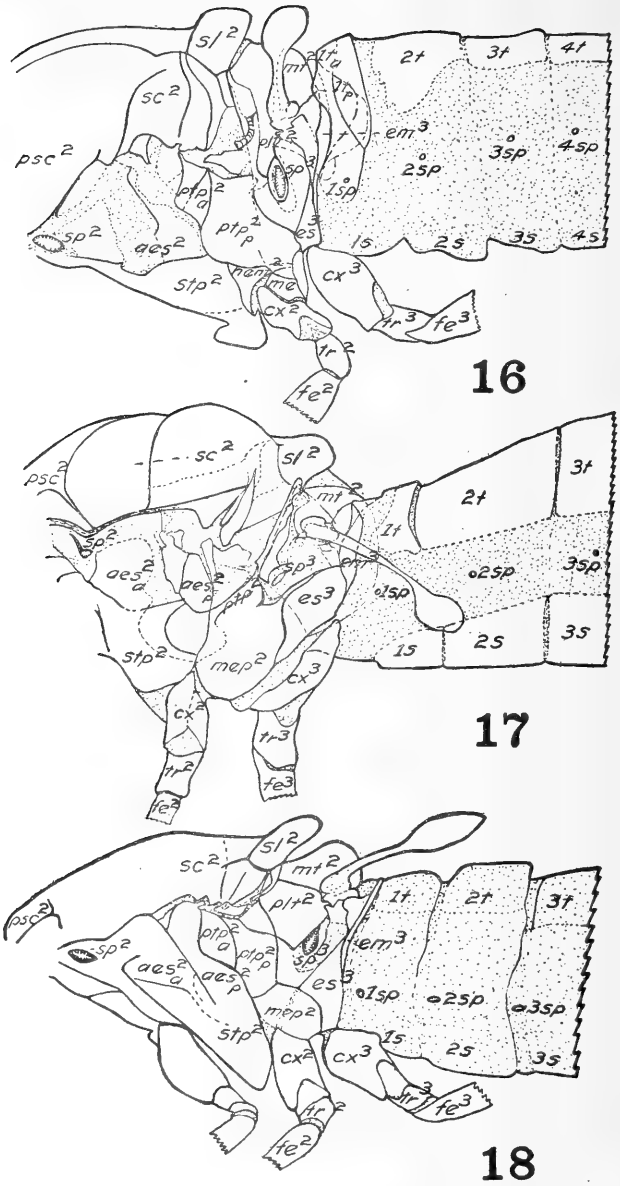
7, *Chironomus ferrugineavitta*, male (Chironomidae). 8, *Chironomus ferrugineavitta, male* (Chironomidae); internal view, showing endothorax. **9**, *Culex canadensis*, male (Culicidae)



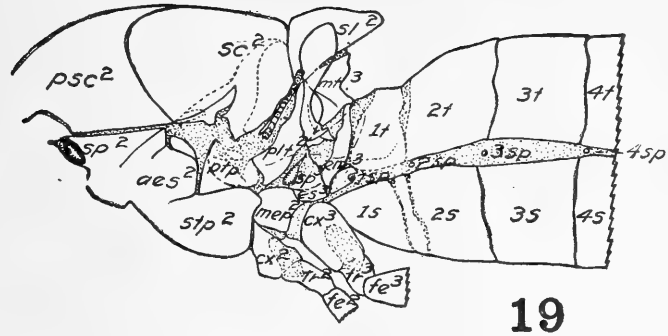
10, *Anopheles quadrimaculata*, female (Culicidae). 11, *Corethra albipes*, female (Culicidae). 12, *Leia winthemi*, female (Mycetophilidae)



13, *Sciara ochrolabis*, male (Sciaridae). 14, *Rhabdophaga strobiloides*, male (Cecidomyiidae). 15, *Plecia heteroptera*, female (Bibionidae)



16, *Simulium hirtipes*, male (Simuliidae). 17, *Blepharocera tenuipes*, female (Blepharoceridae). 18, *Orphnephila americana*, female (Orphnephilidae)



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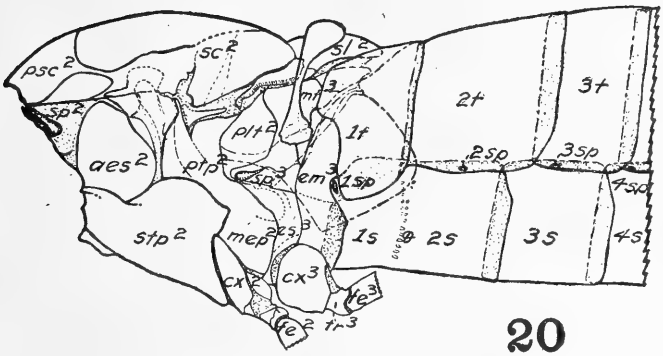

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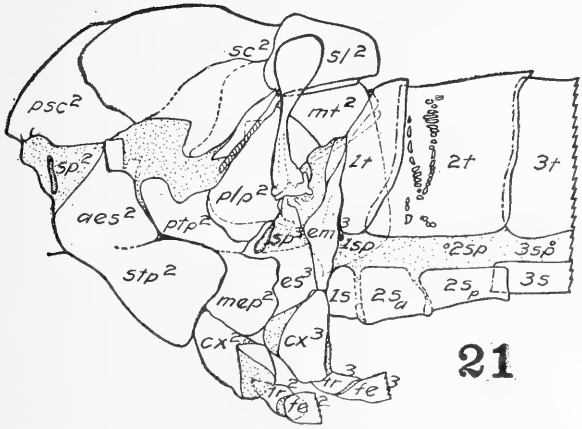
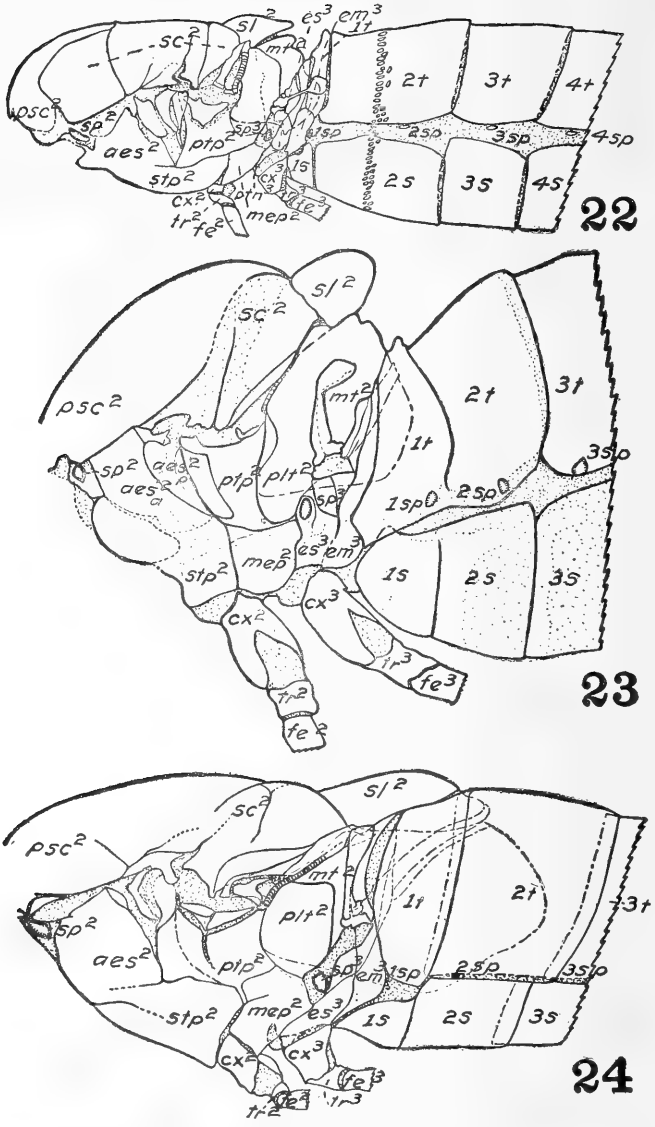
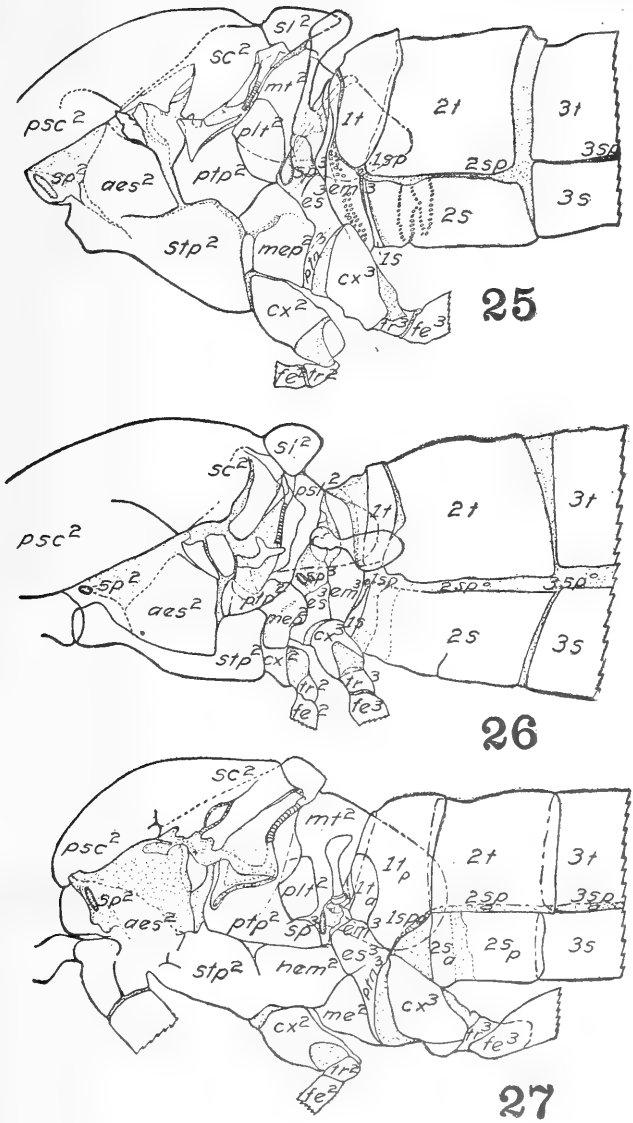


21

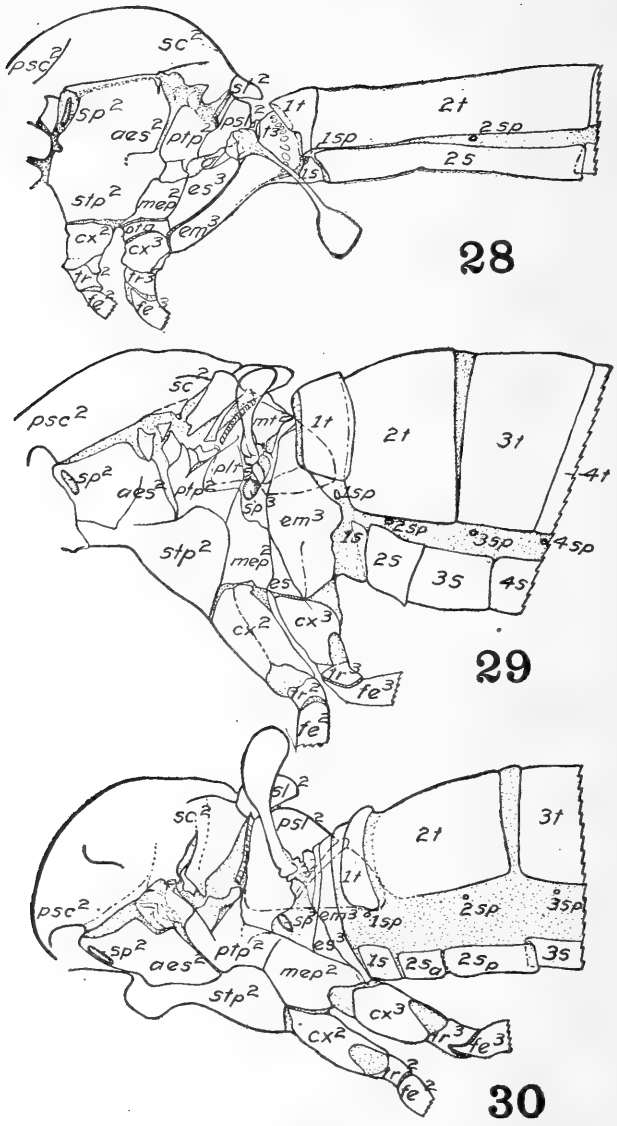
19, *Allognosta fuscitarsis*, female (Stratiomyiidae). 20, *Chrysops indus*, male (Tabanidae). 21, *Chrysopila ornata*, male (Leptidae)



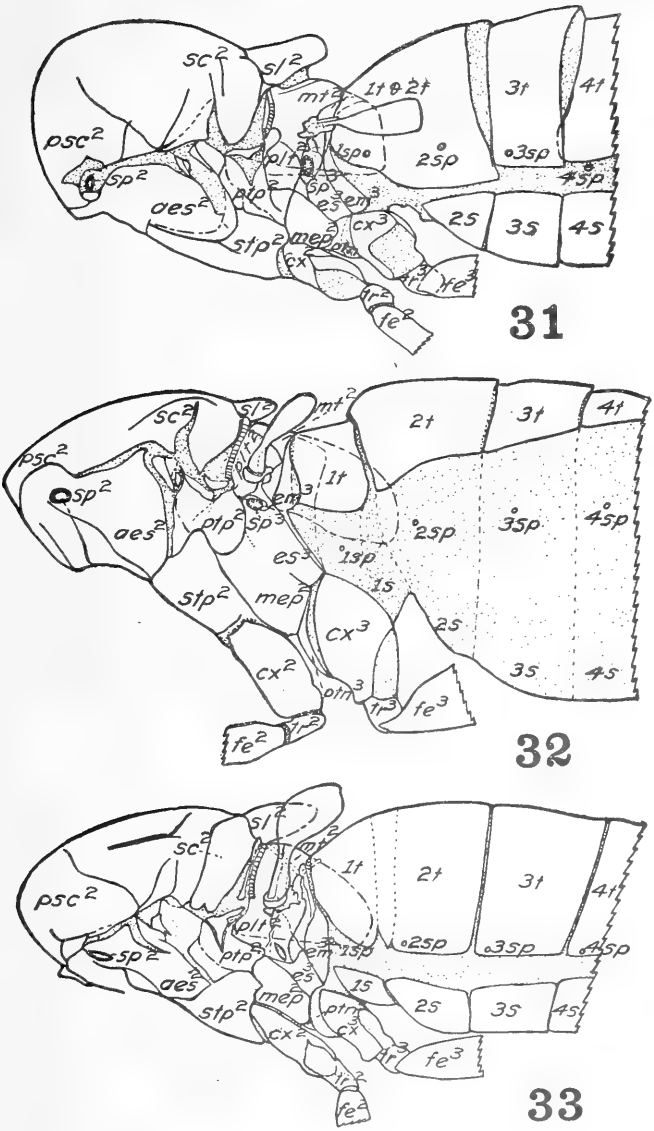
22, *Hirmoneura* sp., female (Nemistrinidae). 23, *Oncodes incultus*, female (Cyrtidae). 24, *Anthrax alternata*, female (Bombylidae)



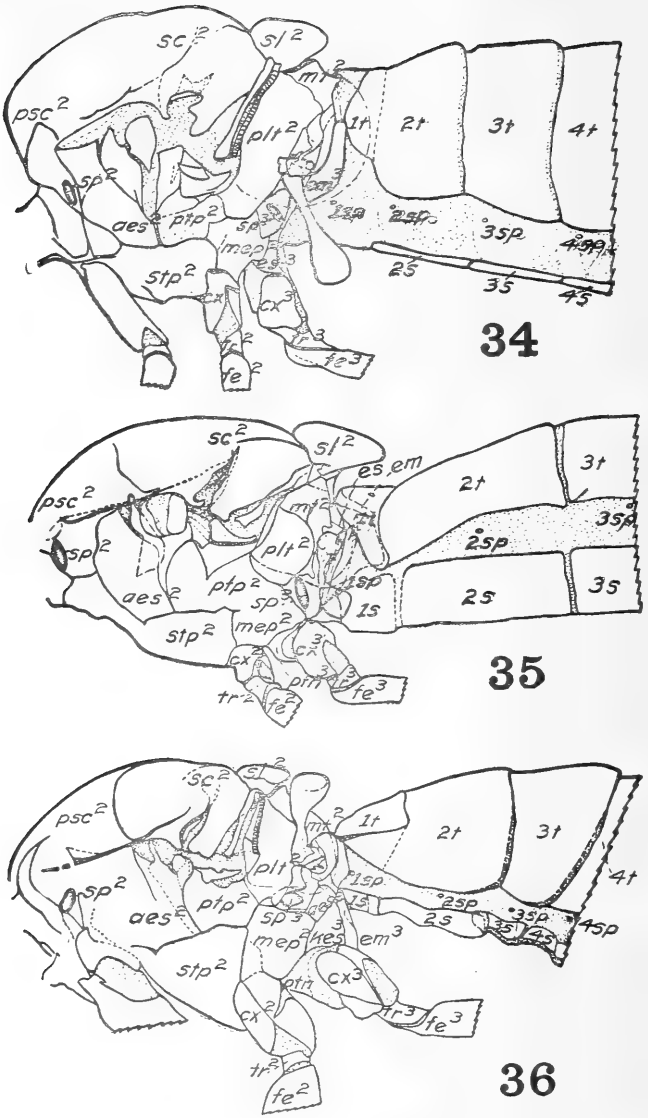
25, *Thereva fucata*, male (Therevidae). 26, *Scenopinus fenestralis*, female (Scenopinidae). 27, *Midas clavatus*, female (Midaidae)



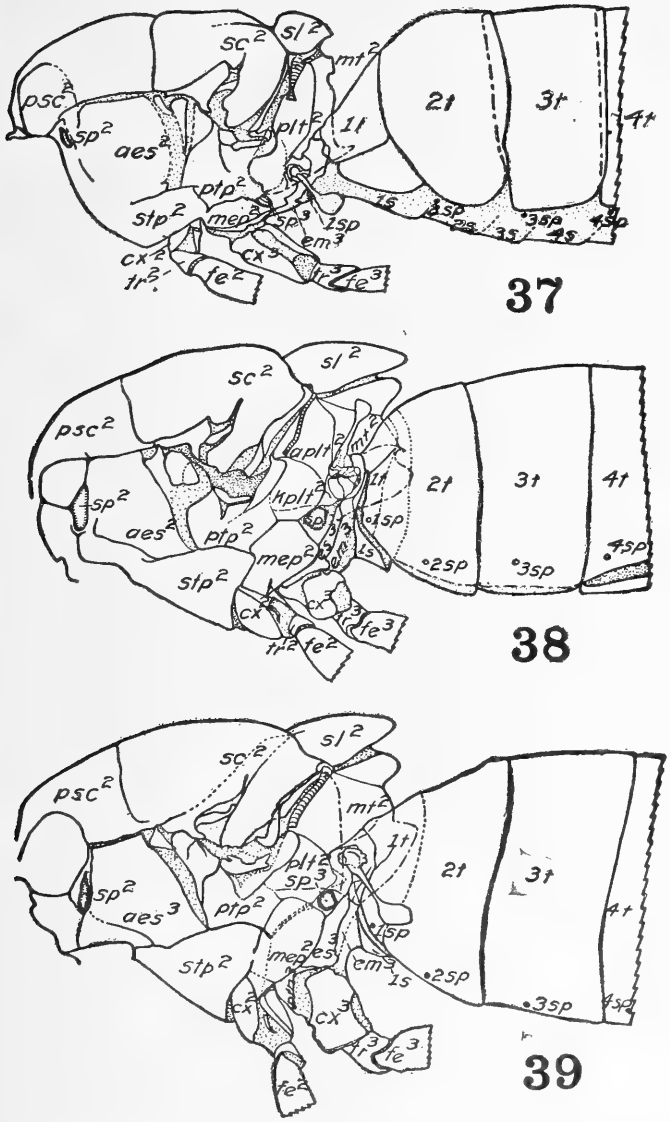
28, *Leptogaster loewi*, female (Asilidae). 29, *Dolichopus cuprinus*, male (Dolichopodidae). 30, *Rhamphomyia* sp., female (Empididae)



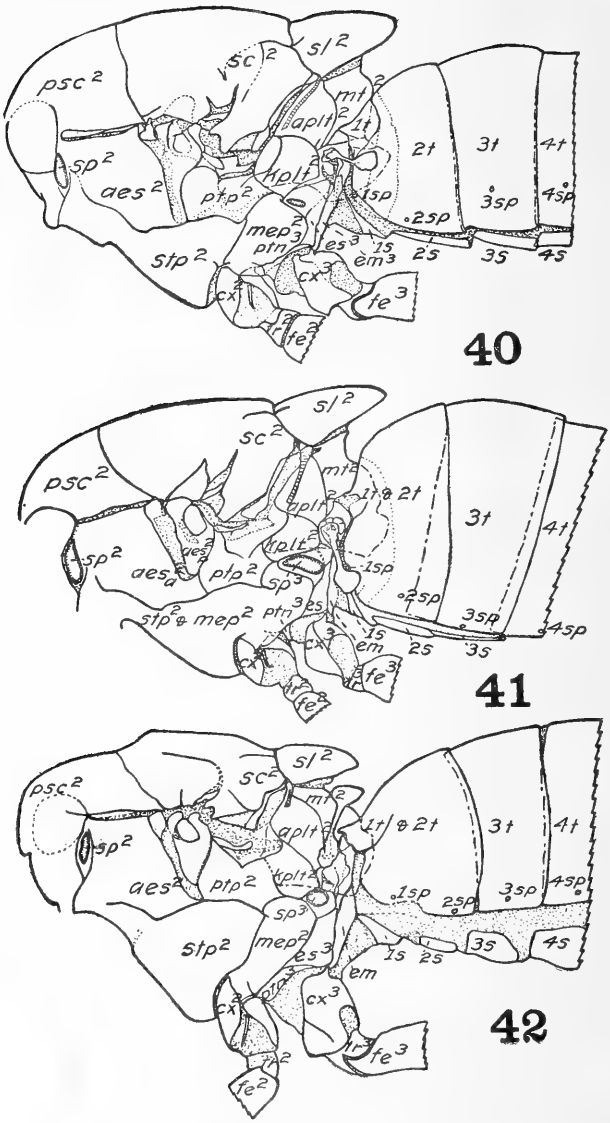
31, *Lonchoptera* sp., female (Lonchopteridae). 32, *Phora concinna* female (Phoridae). 33, *Platypeza velutina*, female (Platypezidae)



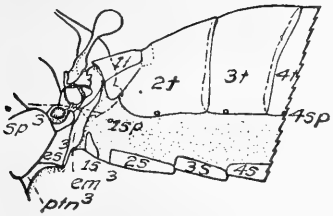
34, *Pipunculus atlanticus*, female (Pipunculidae). 35, *Syrphus americanus*, male (Syrphidae). 36, *Myopa vesiculosa*, male (Conopidae)



37, *Gastrophilus intestinalis*, female (Oestridae). 38, *Tachina mella*, female (Tachinidae). 39, *Thelaira nigripes*, male (Dexiidae)



40, *Sarcophaga communis*, male (Sarcophagidae). 41, *Muscina stabulans*, female (Muscidae). 42, *Macrorchis ausoba*, male (Anthomyiidae)



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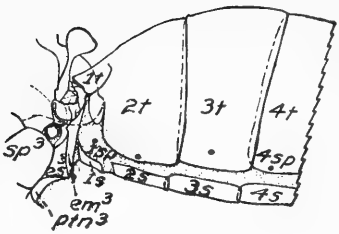

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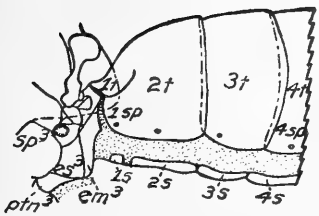

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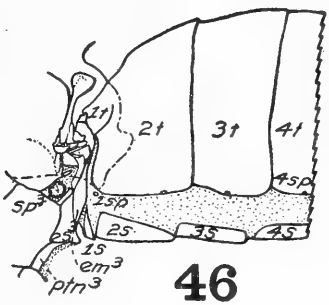

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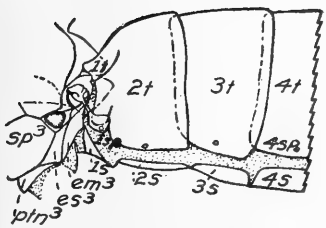

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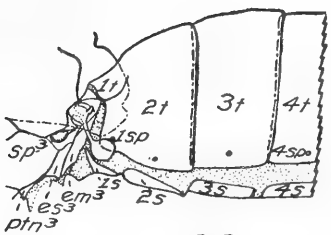

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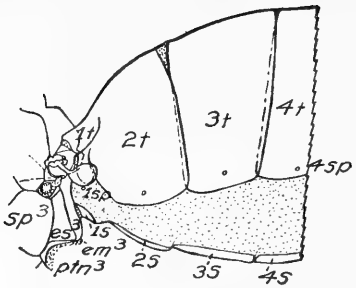
43, *Chortophila cilicrura*, male (Anthomyiidae). 44, *Hylephila paludis*, female (Anthomyiidae). 45, *Schoenomyza dorsalis*, female (Anthomyiidae). 46, *Ophyra leucostoma*, male (Anthomyiidae). 47, *Lispa sociabilis*, female (Anthomyiidae). 48, *Limnophora aequifrons*, male (Anthomyiidae)



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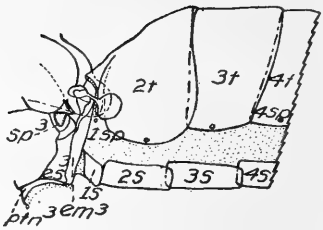

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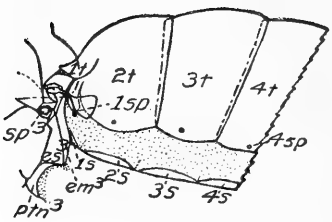

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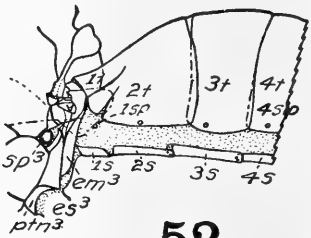

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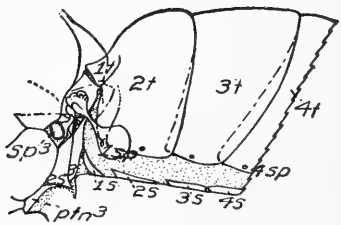

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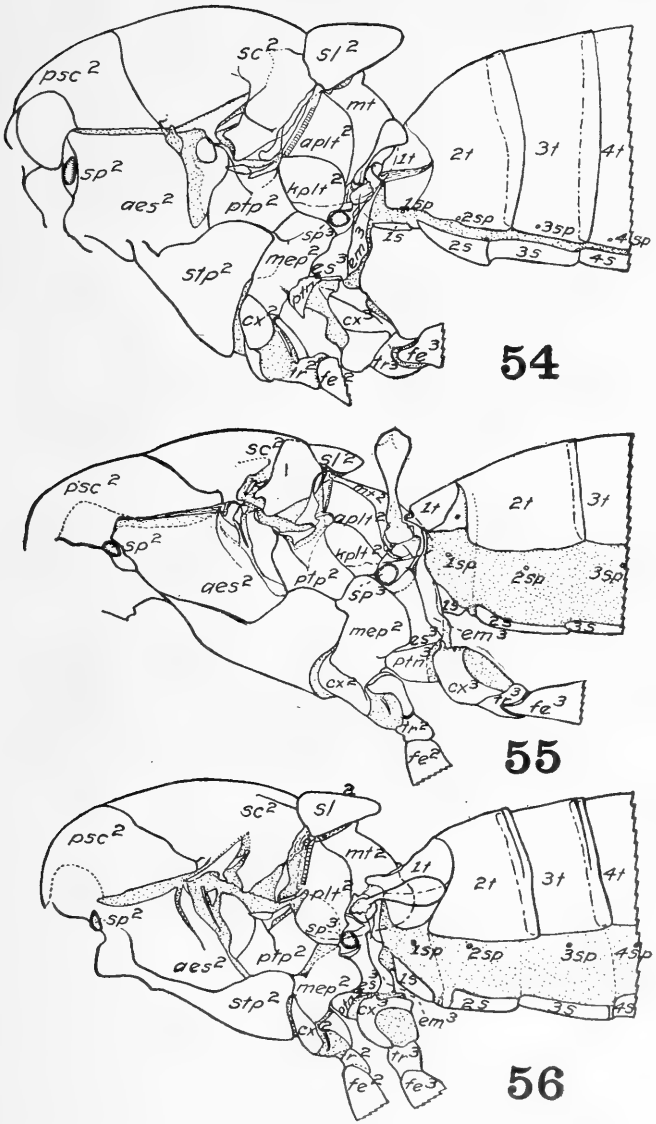
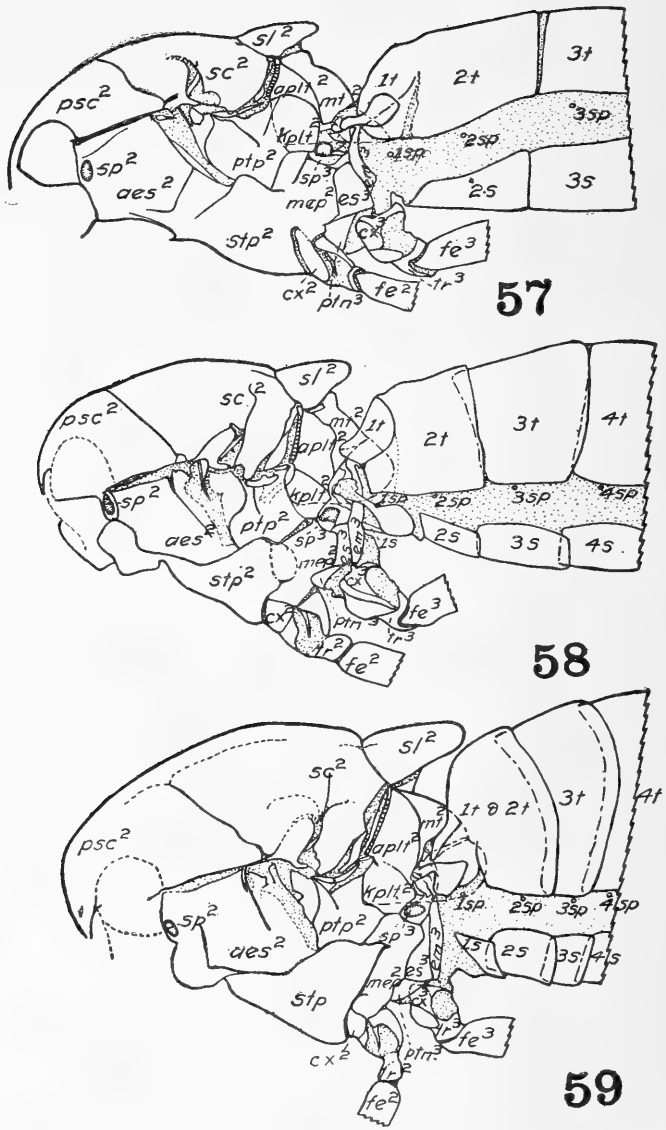
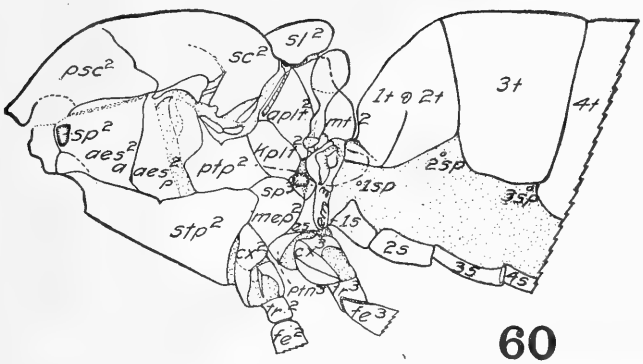
49, *Eremomyia cylindrica*, female (Anthomyiidae). 50, *Pegomyia affinis*, female (Anthomyiidae). 51, *Hylemyia lipsia*, female (Anthomyiidae). 52, *Anthomyia radicum*, male (Anthomyiidae). 53, *Hebecnema umbratica*, female (Anthomyiidae).

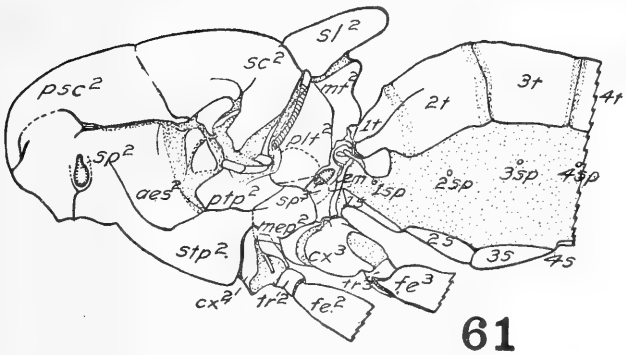


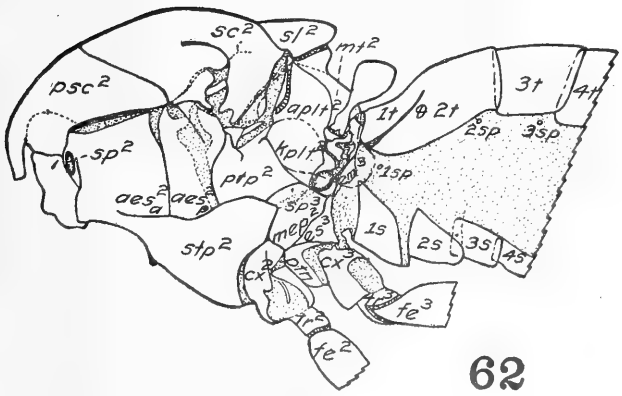
54, *Scatophaga stercoraria*, male (Scatophagidae). 55, *Clusia lateralis*, female (Heteroneuridae). 56, *Leria serrata*, male (Helomyzidae)



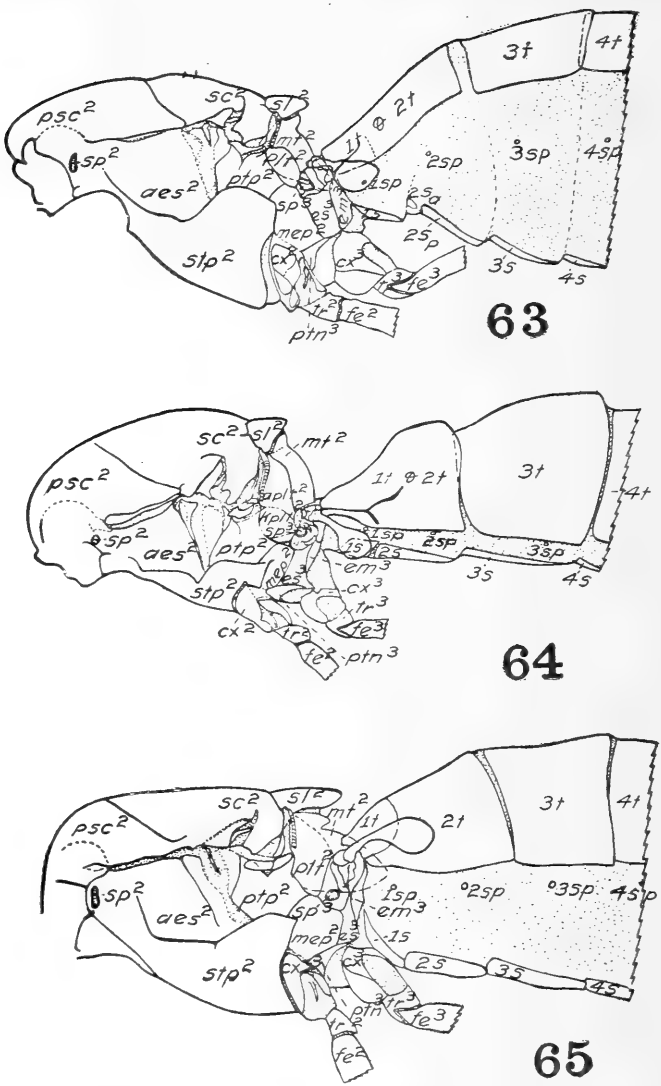
57, *Borborus equinus*, female (Borboridae). 58, *Dictya umbrarum*, female (Sciomyzidae). 59, *Sapromyza lupulina*, male (Sapromyzidae)



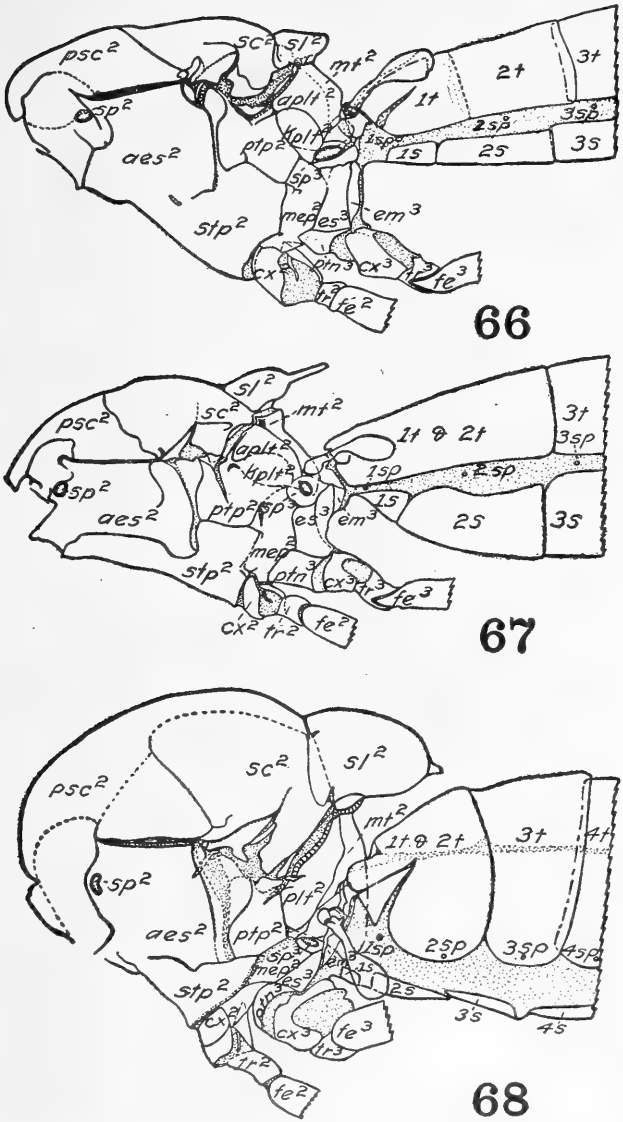




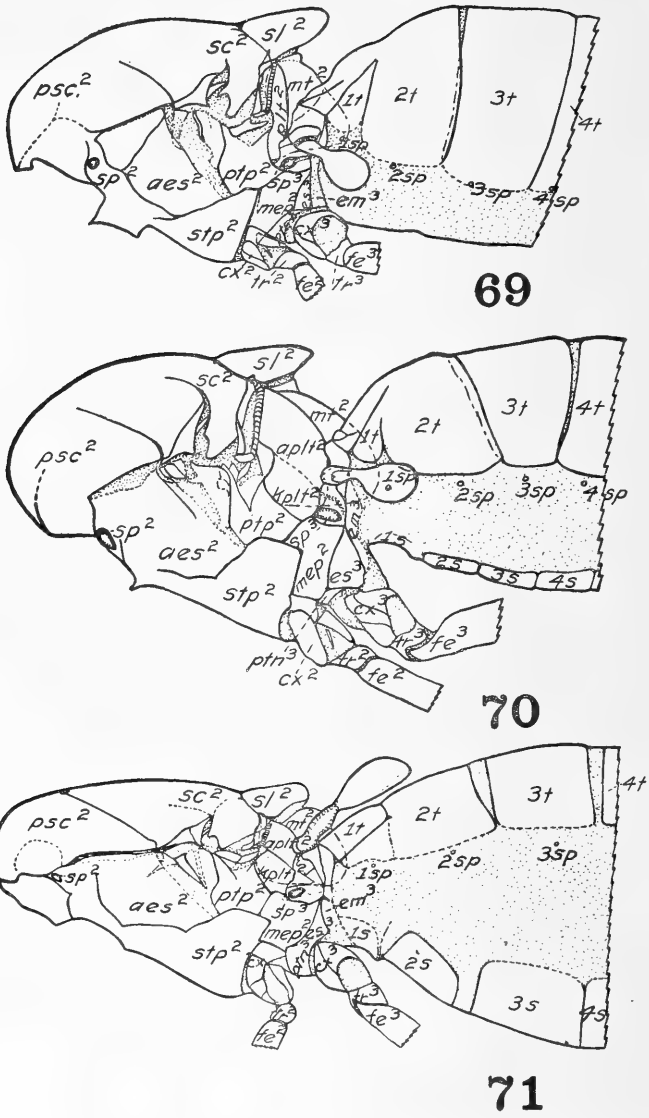
60, *Rivellia viridulans*, female (Ortalidae). 61, *Rhopalomera flaviceps*, female (Rhopalomeridae). 62, *Euaresta festiva*, female (Trypetidae)



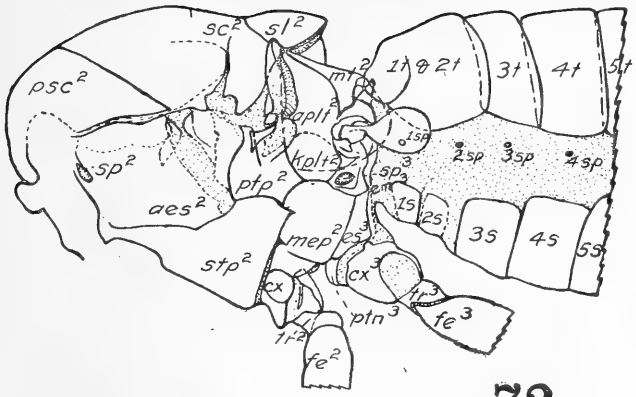
63, *Calobata albiceps*, female (Micropezidae). 64, *Sepsis violacea*, female (Sepsidae). 65, *Piophila casei*, female (Piophilidae)



66, *Loxocera pleuritica*, male (Psilidae). 67, *Sphyracephala brevicornis*, female (Diopsidae). 68, *Parydra limpidipennis*, female (Ephydridae).



69, *Chlorops* sp., male (Oscinidae). 70, *Drosophila melanogaster* (?), female (Drosophilidae). 71, *Anthomyza gracilis*, female (Geomyzidae).



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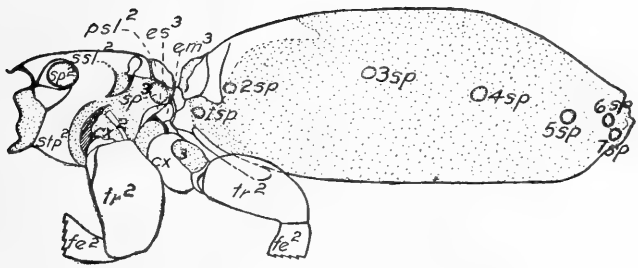

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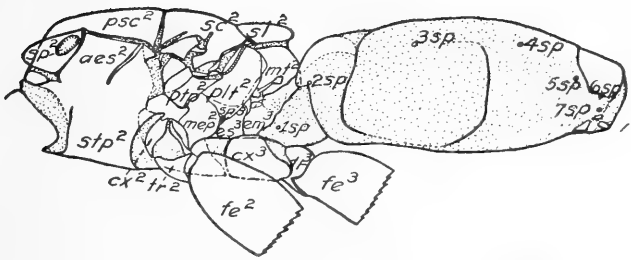

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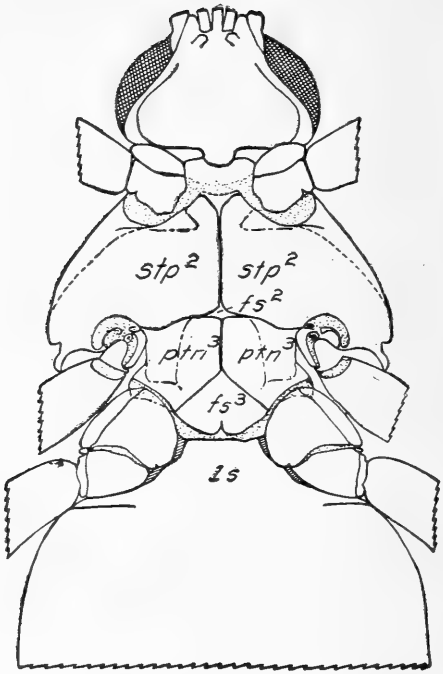
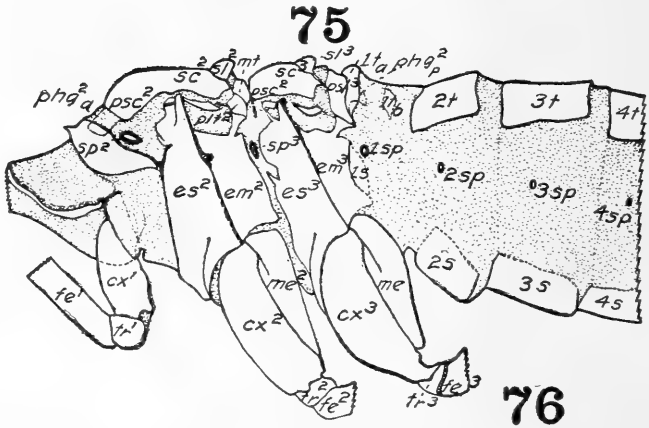
72, *Agromyza lateralis*, male (Agromyzidae). 73, *Melophagus ovinus*, female (Hippoboscidae). 74, *Olfersia americana*, female (Hippoboscidae)





75, *Olfersia americana*, female (Hippoboscidae); **ventral view.**
76, *Panorpa venosa*, female (Panorpidae)

OCTOBER, 1921 MEMOIR 47

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

TYPHA INSECTS: THEIR ECOLOGICAL RELATIONSHIPS

P. W. CLAASSEN

ITHACA, NEW YORK
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CONTENTS

TYPHA INSECTS: THEIR ECOLOGICAL RELATIONSHIPS

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P. W. Claassen

In order that the ecological relationships of the insect fauna of the cat-tail plant may be better understood, the first part of this paper deals with the ecology of the cat-tail plant. In the second part, the life history and biology of the insect inhabitants of the plant are discussed. This part of the paper has been treated from a systematic point of view, considering the insects under their respective orders, rather than grouping them according to their life habits. In the résumé, composing the third part, an attempt has been made to bring out the true ecological relationships, grouping the insects with reference to the parts of the plant they affect, their relative importance, and their interrelations.

ECOLOGICAL STUDIES OF TYPHA

THE SWAMP AREA OF THE UNITED STATES

According to Davis (1911)[1] there are 139,855 square miles of swamp area in the United States, exclusive of Alaska. This includes bogs, marshes, muck lands, and the more typical swamps. The vegetation in these wet lands varies from the semi-floating forms to the wooded plants of the more solid areas. Needham and Lloyd (1916) state that the bogs, marshes, and swamps " occupy a superficial area larger by far than that covered by lakes and rivers of every sort. They cover in all probably [*sic*] more than a hundred million acres in the United States."

Much of the vegetation of this wet area consists of cat-tail (Typha). Many of the marshes contain an almost pure growth of cat-tail, as, for example, the Montezuma Marsh at the foot of Cayuga Lake. This marsh covers an area of approximately 36 square miles. Although it is impossible to give definite figures on the size of the area occupied by cat-tails in the United States, it is safe to say that there are thousands of square miles of wet lands which are covered by either a pure growth of cat-tail or plant associations in which the cat-tail is the dominant form.

Author's acknowledgment. The author is indebted to Professor James G. Needham for his helpful suggestions and criticism in this work.

[1] Dates in parenthesis refer to *Literature cited*, page 508.

PLACES OF STUDY

These studies have been made largely from material gathered in the swamps and marshes around Ithaca, New York, especially from Renwick Marsh, at the head of Cayuga Lake. Other collecting places around Ithaca were Michigan Hollow, Mud Creek Swamp, near Freeville, the McLean Bogs, Vanishing Brook, north of the Cornell University campus, Cascadilla Creek, and various other places, wherever cat-tails were found growing. Observations were made also on the extensive cat-tail marshes of Lake Ontario, at North Fairhaven. During the season of 1916–1917, studies on cat-tails were made also in the vicinity of Lawrence, Kansas.

The Renwick Marsh comprises a field of many acres, of which a large proportion is covered with cat-tail. In some places, this plant grows so thickly that all other vegetation is excluded, and especially is this true of the central part of the marsh, where the soil is much wetter. As one approaches the outer margin, other plants mingle with the cat-tails; and at the border, where conditions are drier, the cat-tail growth is sparse. All the cat-tail patches along the Inlet Valley, up to the Buttermilk Falls region, are referred to as the Renwick Marsh.

Michigan Hollow is a swamp located about six miles from Ithaca, in the Inlet Valley. Cat-tails grow here only scatteringly, in small but rather dense patches. This swamp was visited several times to make collections and observations.

In the McLean Bogs, cat-tails are not found in large numbers, but since these bogs were visited every Saturday throughout the spring and summer of 1916, the author was enabled to make more careful and complete observations of the conditions and life histories of the insects of the cat-tail plants there found. Moreover, where cat-tails are not so abundant, a higher percentage of infestation usually occurs, which renders it much easier to obtain material and to make comparative studies.

The Mud Creek Swamp is an old swamp extending along Mud Creek, near Freeville. Here, also, the cat-tails grow but sparingly, but it was found easy and convenient to make frequent observations and collections of material.

Along Vanishing Brook, north of the Cornell University campus, there are a number of small patches of swampy ground, on which cat-tail plants

may always be found. On account of its nearness to the laboratory, this was found to be a convenient place to make some of the observations.

Occasional cat-tail plants are also found in Bool's Back Water and in Cascadilla Creek, two places which were likewise chosen for study because their close proximity to the laboratory made daily observations possible.

THE SPECIES OF TYPHA

According to Britton and Brown (1913) there are about ten species of Typha in the temperate and tropical regions of the world. In the United States there are at least two species represented, *Typha latifolia* L. (type species) and T. *angustifolia* L. Dudley (1886) lists *T. latifolia* L., var. *elongata*, n. var., as a variety occurring in New York. He describes it as follows: "Leaves very numerous, dark green, elongated (2–3½m.) and fruiting spike elongated, often 30 cm."

Typha latifolia has broad leaves. The staminate and pistillate parts of the flower spike are contiguous. The stigmas are spatulate or rhomboid. Pollen grains occur in fours. Pistillate flowers are without bractlets.

Typha angustifolia has narrower leaves than *Typha latifolia*. The staminate and pistillate flowers of the flower spike are usually separated by a short interval. The stigmas are linear or oblong-linear. Pollen occurs in simple grains. The pistillate flowers have bracts.

Typha is known by the following common names: cat-tail, great reed mace, cat-o'-nine-tail, cat-tail flag, cat-tail rush, flax tail, blackamoor, blackcap, bullsegg, bulrush, watertorch, and candlewick. The names "marsh beetle" and "marsh hog" have also been applied to the Typha plant.

THE DISTRIBUTION OF TYPHA

Cat-tails are common in the temperate and tropical regions of America, South America, Europe, and Asia. Wherever favorable soil conditions occur, cat-tails will be found growing; even a spring on the hillside or the outlet of a drain pipe will sometimes support a few of the plants. Large patches of them grow in the Rocky Mountains, at an altitude of 7500–8500 feet. *Typha latifolia*, the commonest of all the species, occurs throughout the United States in any favorable location. *Typha latifolia* grows abundantly throughout North America, except in the extreme

North. *Typha angustifolia* grows abundantly in the marshes along the Atlantic Coast from Nova Scotia to Florida, as well as inland and even in California.

GROWTH HABIT AND REPRODUCTION

Cat-tails are marsh or aquatic plants, with creeping rootstocks, fibrous roots, and glabrous, erect stems. They are perennial plants, the rootstocks remaining alive while the stem dies down to the ground every year. The following spring these rootstocks, or rhizomes, send up the new plants. Plants which attain only partial growth during the season keep the center alive that winter and probably reach maturity the following summer. The rhizomes spread in every direction and within a few years a large group of cat-tails results from the offsets of a single plant. It is really very difficult to define the limits of a single plant, since they are so linked together by these underground rhizomes (Plate XLV, 56). A two-years growth of a plant, with the connecting rhizome and the offset which will form the next season's stalk, is shown in Plate XL, 18.

Aside from the vegetative mode of increase, Typha produces a great number of seeds each year. These seeds are provided with pappus, which carries them far abroad and insures seeding in all possible situations. In *The Book of Nature Study* (Farmer, 1902–10), the following statement occurs: "When they [the fruits] become detached from the spike, the hairs borne by the stalk of each fruit act as wings to disperse the seed; the hairs fluff out into downy masses, so that the whole spike looks about a hundred times as large, for a single head will contain a quarter of a million of these flying seeds, according to Professor Lloyd Praeger's estimate." .

In order to determine somewhat accurately the number of seeds produced by one head of *Typha latifolia*, the number of seeds in four dry, mature heads was determined. For this work an analytical balance was employed. The procedure was as follows: First, each head was weighed entire; then a small bunch of the seeds was detached and weighed, after which the number of seeds in this bunch was counted; finally, all the seeds were removed and the rachis alone was weighed. From the figures so obtained, the number of seeds in each of the heads was computed (table 1), and the number of seeds in the average Typha head was found to approximate 250,000.

TABLE 1. COMPUTATION OF THE AVERAGE NUMBER OF SEEDS IN EACH TYPHA HEAD

	Sample 1	Sample 2	Sample 3	Sample 4
Length of head (millimeters)	160	180	180	160
Weight of entire head (grams)	35.6735	30.5632	35.2700	27.1150
Weight of rachis (grams)	2.8330	1.9480	2.1610	1.6850
Weight of seeds minus rachis (grams)	32.8405	28.6152	33.1090	25.4300
Weight of detached bunch of seeds (grams)	0.0179	0.0490	0.0400	0.0400
Number of seeds in detached bunch.	167	480	300	295
Estimated total number of seeds in head	306,393	280,320	248,317	187,546

Average number for the four heads, 255,644.

GERMINATION OF TYPHA LATIFOLIA

The manner of germination of *Typha latifolia* is very unusual. The development of the plant from the seed was observed in the laboratory. The seeds were placed in watch glasses and could thus be studied under the binocular microscope from day to day. Some of the watch glasses contained only water in which the seeds germinated, while in others a little soil was placed in the bottom in order to observe the growth of the roots. The watch glasses were kept covered to prevent evaporation. The seeds, when first thrown upon the surface of the water, remained floating. Soon, however, the pericarp broke open and the little seeds sank to the bottom.

The seeds are much elongated, pointed at one end and at the other closed by a cone-shaped trapdoor, or cap (Plate XXXIX, 3). The general appearance of the seed is not much unlike some of the insect eggs which are closed at one end with a capsule-like cover. Ten seeds of *T. latifolia*, chosen at random from two heads, were removed from the pericarp and the length and diameter of each was carefully measured (table 2). The average length of the seed was found to be 1.339 millimeters, and the average greatest diameter, 0.307 millimeter. The surface of the seed is sculptured with small, branching ridges, starting at the end of the cap and branching as they run down to the other end. The entire seed, including both its pericarp and its pappus, is about 10 to 12 millimeters long. The pappus consists of from 15 to 20 white hairs, attached to the base and lower quarter of the stalk (Plate XXXIX, 1 and 2).

TABLE 2. MEASUREMENTS OF THE SEEDS OF TYPHA LATIFOLIA

Specimen	Length (millimeters)	Diameter (millimeters)
1	1.50	0.29
2	1.21	0.25
3	1.42	0.28
4	1.35	0.28
5	1.42	0.37
6	1.05	0.28
7	1.42	0.37
8	1.42	0.37
9	1.45	0.28
10	1.15	0.30
Average	1.339	0.307

When germination begins, the cotyledon lengthens and pushes out through the trap door. Sometimes the cap is carried away on the tip of the developing embryo, but more often it remains attached as if by a hinge to the seed. The embryo, immediately after emerging from the seed, turns downward toward the bottom of the dish. Growth is very rapid. Hardly has the embryo come out of the seed before the epidermal cells near the tip begin to send out slender root-hairs, which help to fix the plant to the bottom soil. The other end of the embryo, or cotyledon, remains in the seed, absorbing the reserve starchy material, the only food of the young, developing embryo (Plate XXXIX, 5). When the embryo has become about twice or three times the length of the seed, the growing tip pushes out the first root (Plate XXXIX, 8). The root also bears a number of the root-hairs. With the exception of the ones at the tips of the roots, these root-hairs disintegrate as the plant further develops. At about the same time that the first root appears, the formation of the second leaf may be seen at the crown of the young plant (the outpushing embryo or cotyledon is considered the first leaf). This second leaf soon penetrates the epidermal cells of the first leaf, and comes out to grow and function as a true leaf (Plate XXXIX, 9). After all the food material in the seed has been absorbed, the tip of the first leaf either disintegrates and is thus loosened from the seed, or the tip of the leaf is withdrawn from the seed (Plate XXXIX, 10). The successive stages of the growth of the plant are shown in Plate XXXIX, 4–10.

Not every seed in the head of *Typha latifolia* is perfectly formed or fertile. A number of them never become fully mature, and therefore could not possibly germinate. It is an easy matter to distinguish the fertile seeds in a mature head from the sterile ones. The mature fertile seeds lie in a closely fitting pericarp, while the sterile ones are inclosed in a pericarp which is developed to more than twice the natural size and which has a "hollow" interior with the kernel undeveloped (Plate XXXIX, 1).

In order to determine the approximate percentage of fertility in the seeds of *Typha latifolia*, a number of seeds were picked off at random from several heads and by a careful examination the number of fertile and sterile seeds was determined. The results of these counts are shown in table 3, where it appears that about 75 per cent of the seeds on the mature heads are fertile. The heads from which these counts were made were picked at random and should represent about average conditions. The third head had nearly half of the seeds sterile; the fourth, however, had a high percentage of fertile seeds.

TABLE 3. DETERMINATION OF THE APPROXIMATE PERCENTAGE OF FERTILITY OF TYPHA SEEDS

Head	Number of seeds counted	Number of seeds fertile	Number of seeds sterile	Per cent fertile
1	300	233	67	77.7
2	200	156	44	78.0
3	250	140	110	56.0
4	250	211	39	84.4
Total	1,000	740	260	.....
Average per cent fertile	.....	.....	.....	74

Having thus ascertained the approximate percentage of fertility in the seeds, experiments were conducted to determine the percentage of germination of the fertile seeds. The seeds were placed in covered watch glasses, and, though kept in the light, were protected from direct sunlight. Germination commenced within a few days after the seeds had been placed in the water. Careful counts were made of the number of seeds

that germinated in each of the watch glasses. The results are shown in table 4. These figures would indicate that not more than two-thirds of the fertile seeds germinate under experimental conditions. Calculating, then, from the percentage of fertility and the percentage of germination, as given in tables 3 and 4, a head containing 250,000 seeds might actually give rise to 125,000 new plants — a 50-per-cent efficiency in reproduction.

TABLE 4. DETERMINATION OF THE PERCENTAGE OF GERMINATION OF FERTILE SEEDS

Head	Number of seeds	Number of seeds germinated	Number of seeds sterile	Percentage of germination
1	20	12	8	60.0
2	50	34	16	68.0
3	18	12	6	66.6
4	73	37	36	50.6
Total	161	95	66	.....
Average per cent germinated	.....	.....	.....	60.5

TYPHA AS A COMMERCIAL ASSET

The vast areas of cat-tail have as yet been little utilized. The plant is rich in starch and other food values and grows in situations now regarded as waste lands. It would yield great quantities of supplies, if only a definite use for it could be found. The Indians and a few other races have used cat-tail products for various purposes. Hooker (1876) says:

> The starchy rhizome of Typha possesses slightly astringent and diuretic properties, which led to its use in East Asia for the cure of dysentary, urethritis, and aphthae. The stems and leaves are used for thatching cottages. It has been vainly tried to utilize the bristles of the spike in the manufacture of a sort of velvet. [The pollen of Typha is made into bread by the natives of Scind and New Zealand.]

Engler and Prantl (1889) say: "The rhizome, rich in starch, may serve as food material; the leaves of several species are used for weaving. The pollen, which is easily recognized by the occasional tetrads, serves at times as surrogate for lycopodium powder."[2]

[2] Translation from the original German.

Parker (1910) speaking of the plants used for food by the Indians, says: "The roots of the cat-tail were often used. Dried and pulverized the roots made a sweet white flour useful for bread or pudding. Bruised and boiled fresh, syrupy gluten was obtained in which corn meal pudding was mixed."

Muskrats are very fond of the rhizomes of the cat-tail, and in the cat-tail swamps the muskrats are accordingly found in large numbers. The leaves of the cat-tail are used to some extent in the manufacture of barrels. On account of their spongy structure, the dried leaves, placed between the staves, expand greatly when moistened, thus making the barrels water-tight. The leaves are also used for chair bottoms. (Dudley, 1886).

The rich starch content of the plant is especially concentrated in the rhizomes, where the cells of the rhizome core (Plate XLV, 57 and 60) are completely filled with small starch granules. This is true of the rhizomes in their dormant or winter conditions (Plate XL, 13). If, however, one examines the cells later in the season, after the plant has attained a growth of several feet, the cells are found to be only partially filled with starch granules, much of the starch having been used up in the rapid early growth of the plant (Plate XL, 15). This fact, showing that they have a much greater concentration of starch during the dormant season than during the growing season, has a direct bearing upon the possible uses of the rhizomes, and any attempts made for the utilization of the starch should be made on the dormant rhizomes. The possibility of utilizing the Typha plant as a source of food has been discussed by the author in another paper (Claassen, 1919).

THE INSECT FAUNA OF TYPHA

The insects which are found on cat-tail have not hitherto been studied as a group. Most of them have been recorded as inhabiting cat-tail, but very little has been published on their detailed life histories and ecological interrelations.

The following discussion includes only those insects which have been found on cat-tail and studied during the course of this investigation. It includes six species of Lepidoptera, two of Coleoptera, eight of Hemiptera, five of parasitic Hymenoptera, and four of Diptera.

LEPIDOPTERA[3]

Arzama obliqua Walk.

Arzama obliqua Walk., a moth of the family Noctuidae, has been known in the adult stage for more than half a century. The species occurs throughout eastern United States and Canada, its host plant being *Typha latifolia*. In New York, near Ithaca, the writer has taken specimens from the following places: Michigan Hollow, Renwick Marsh, Bool's Back Water, McLean Bogs, Cascadilla Creek, and Ringwood Hollow.

Life history and habits

The life history of this insect is unusual and interesting from an ecological point of view. There is only one generation a year. The full-grown larva passes the winter in its burrow in the plant.

Egg-laying.— The eggs are laid on the surface of one of the first-formed leaves of *T. latifolia*, from six to fifteen inches below the tip. This later becomes one of the outer leaves of the plant. The eggs are placed on the leaf several layers deep. The lower layer covers the largest area and contains from twenty-five to forty eggs, while the upper layers cover only the central part of this bottom layer, forming a gradually sloping mass and containing from ten to twenty eggs in the two or more upper layers. The total number of eggs in one egg mass varies from thirty-five to sixty. The whole egg mass is covered with a thick layer composed of a mixture of froth, hairs, and scales from the body of the female. The egg mass greatly resembles a mass of spider's eggs (Plates XLI, 24 and 25, and XLVI, 65). It is of a dirty, yellowish-white color. It measures from twelve to fifteen millimeters in length, from seven to ten millimeters in width, and from three to four millimeters in height at the center. In shape it is oblong and convex, the edges gradually thinning out and adhering closely to the surface of the leaf. The long axis of the egg mass corresponds to the long axis of the leaf.

One female apparently lays several egg masses. In dissecting out the ovary of one female, 225 eggs were found, all fully formed and developed; and since only thirty-five to sixty eggs occur in a single mass, this indicates that one female may deposit about half a dozen egg masses.

[3] The Lepidoptera mentioned in this paper have all been determined by Dr. W. T. M. Forbes.

Usually only one egg mass occurs on the same leaf, but sometimes two, and in one instance three, masses were found on a single leaf. It is not uncommon to find two or three leaves of the same plant with an egg mass on each of them.

In the spring of 1918, careful observations were made for the appearance of the adults or the egg masses on the plants. In the laboratory, where moths had been bred, they failed to mate or to deposit eggs in the characteristic manner. A few females did lay infertile eggs on the stems and leaves of Typha. Egg masses were first noticed in the field on May 26. After this date new egg masses were constantly found until June 8. The height of egg-laying was between May 26 and June 2. At the McLean Bogs the egg masses appeared about six days later than those at the places around Ithaca.

The larva.— On turning the egg mass over, after the larvae have hatched, the empty egg shells are disclosed. The hatching process does not disturb the egg mass in the least. Without devouring the egg shell, the embryo breaks through it and bores directly into the leaf of the cat-tail, where it works as a leaf miner. This manner of hatching seems to be an excellent protective adaptation against egg parasites and other enemies. The mass is practically impervious to water. Thus from the time the egg is laid to the time when the larva hatches and enters the leaf to become a leaf miner, it is not once exposed to the direct dangers of enemies or of weather conditions.

Once the larvae enter the leaf, they begin their work as typical leaf miners. The structure of the leaf of the cat-tail plant is rather peculiar. The fibro-vascular bundles are found mainly in longitudinal, I-like partitions. This produces a loose inner structure with many large air spaces (Plate XL, 11). The longitudinal partitions are again traversed by transverse partitions which also are composed of parenchyma. A leaf of Typha with the epidermis removed to show this inner structure appears in Plate XLV, 58. When the larvae have entered the leaf, they begin to mine, mostly downward, scraping off the chlorophyll from the upper and lower epidermis of the leaf. They eat out the transverse partitions, leaving the longitudinal partitions and the fibro-vascular bundles undisturbed except when occasional larvae cut through to get in other channels. A few of the larvae may first mine upward toward the tip of the leaf, but soon they all proceed downward, moving abreast along the

channels. As many as eight larvae have been found together in one channel. It is probably due to such a crowded condition that a larva occasionally crosses over into another channel.

After the larvae have mined down for a distance of twenty to twenty-four inches, they molt in the mines and immediately afterward leave the mines through a little exit hole which is usually made on the inner side of the leaf. As soon as the larvae appear on the surface of the leaf they at once seek shelter, usually continuing down the stem of the plant and crawling behind the sheath of one of the outer leaves.

Since the larvae later become true stem borers, the question arises why they should come out of the mines of the leaf ten or fifteen inches away from the stem instead of remaining in the mines and working down the leaf until they reach the stem and can enter it directly. There are two plausible reasons against such behavior: first, the larvae later become solitary borers and after coming out of the leaf they separate and individually enter the stems of different plants; second, the width of the head of the second-instar larva exceeds the width of the average longitudinal channels in the cat-tail leaf. Careful measurements of the molted heads of the first-instar larvae and measurements of the width of the average channel of the leaf showed that the width of the head during the first instar was only slightly less than the width of the channel. The width of the heads of the second instar was considerably wider than the width of the channels of the leaf. Following are the average measurements:

Width of head of first-instar larva.....	0.597 millimeter
Width of head of second-instar larva.....	0.90 millimeter
Width of channel in leaf.....	0.62 to 0.72 millimeter

It would therefore be impossible for the larvae to remain in the leaf after the first molt unless they widened the leaf by taking out the longitudinal fibrous partitions.

Although the larvae ultimately become solitary stem borers, they do not always scatter immediately after emergence from the mines and bore directly into the stems of the plant. In one instance, on June 29, 1916, it was found that a whole contingent of larvae had migrated to the head of the plant, where they found shelter behind the leaves that were sheathing the flower spike. Here they were feeding on the staminate flowers. A few days later they had all descended and scattered to different

plants. It is probable that such a migration to the flower spike was accidental; on the other hand, it may have been because the plant had a central stalk with a flowering spike that the larvae could not or would not enter it, for the writer has never found that they bored into a plant which had a flower stalk, nor has he ever found a plant in which the stem borers occurred producing a flower stalk.

The larvae enter the stalk from behind the sheath after they leave the leaf, and there they feed for some time. Only once were two larvae found in the same burrow. They normally become solitary borers, tunneling through the center of the stem, going downward to the crown, and sometimes even advancing for a short distance into the rhizome. This tunneling causes the central leaves of the plant to die, and consequently no flower spike is formed. The affected plants are easily recognized by the presence of the dead central leaves.

The larvae grow rapidly and by late fall have attained a length of nearly two inches. They leave the burrow full of the frass and the shreds of the fibrous tissue torn loose by their passage. In the fall, before the larvae go into hibernation, they eat out an exit hole in the stem, four to six inches above the ground, which they loosely plug up with frass and fibrous material. They then make a little compartment, or cell, by closing the burrow above and below with a mass of frass and fibrous material, as shown in Plate XLI, 27 and 28, and thus pass the winter. If one visits the marshes in winter and opens the plants, the larvae are found in the burrow, completely surrounded by ice. Larvae taken to the laboratory during September and October and placed in metal salve boxes on moist, sterilized sand, pupated in February and March. Adults emerged from sixteen to twenty days later. Larvae brought into the laboratory in the spring pupated much later, as is shown by table 5.

In the laboratory, several days before the larva transforms to the pupal stage, it begins to spin a thin, irregular layer of fine thread all over the surface of the sand in the salve box. In the field, one finds these loose webs lining the burrows in the stalks. The larva then becomes very sluggish and gradually shortens until it seems only about half of its normal length. The shiny, almost black, larval skin becomes much lighter in color. This is a sign that pupation will occur within twenty-four to

thirty-six hours. When the larva is ready to pupate, the larval head splits along the epicranial suture and the skin breaks open on the median dorsal line, along the first two thoracic segments, extending also about three-fourths of the way across the third thoracic segment. Gradually the skin slips off backward until the newly formed pupa is free. The pupa is at first entirely white except the cremaster, which is dark brown.

TABLE 5. LENGTH OF PUPAL PERIOD OF ARZAMA OBLIQUA

Specimen	Date of pupation	Date of emergence	Sex	Length of pupal stage (days)
1	February 21	March 11	Female	18
2	March 4	March 22	Male	18
3	March 10	March 29	Female	19
4	March 21	April 7	Male	17
5	March 25	April 11	Female	17
6	March 25	April 12	Female	18
7	March 25	April 11	Female	17
8	March 26	April 12	Female	17
9	March 28	April 14	Female	17
10	March 29	April 14	Male	16
Average length of pupal stage				17.6

TABLE 6. MEASUREMENTS OF PUPAE OF ARZAMA OBLIQUA*

Specimen	Females		Males	
	Length (millimeters)	Width (millimeters)	Length (millimeters)	Width (millimeters)
1	33.0	7.0	29.0	7.0
2	35.0	8.5	28.5	6.5
3	31.5	6.5	28.0	6.5
4	30.5	7.5	.....	.....
5	31.5	6.8	.....	.....
6	35.5	8.0	.....	.....
7	33.0	7.0	.....	.....
Average	32.85	7.25	28.5	6.7

*The measurements of the pupae of *Arzama obliqua* were taken as follows: length, from the anterior end to the tip of the cremaster; width, the greatest lateral width of the pupa.

The first color of the body appears on the dorsal surface of the meso- and metathorax and on the first and second abdominal segments. After about ten minutes more the entire abdomen begins to assume a reddish color, the thorax, head, and wings still remaining nearly white, however. The pulsation of the dorsal vessel is very noticeable at this time. At the end of another twelve minutes the color is darkest on the sixth, seventh, and eighth abdominal segments, being more pronounced on the dorsal surface. Twelve minutes later the head begins to show color. In another half hour the entire pupa, except the wings, has become a reddish brown in color. The wings, which remain white the longest, now begin to show a little color. Later the pupa turns very dark brown, almost black.

Description of the stages

The egg

Light yellowish in color; round, though somewhat flattened, with the micropyle on the upper side, away from the surface of the leaf (Plate XLI, 21). 1 to 1.2 mm. in diameter and 0.8 mm. in height. Sculpturing very fine but quite characteristic; micropyle represented by a small dot surrounded by a rosette of about twelve elongate cells. This surrounded in turn by two other rings of more or less elongate cells; a reticulation following, with cells more or less regularly hexagonal; and, finally, the outside cells slightly elongated transversely. Entire reticulate area around the micropyle covering about two-thirds of the upper surface of the egg. Remainder of egg sculptured with a number of small tubercles, some occurring in lines so as to suggest circumferential bands of tubercles.

The first-instar larva (Plate XLI, 29)

Length 3.43 mm., width 0.58 mm. across the head. Head light brown, labrum and eyes darker. General color white, with a median purplish stripe. Spiracles on the eighth abdominal segment very large and dorsally located, as in the full-grown larva. After larva has been feeding for a few days, general color yellowish green.

The full-grown larva (Plates XLI, 22, and XLVI, 66)

Length 50 to 60 mm., width 6 to 7 mm. General color shiny muddy black. Head very dark brown. Lower half of clypeus light yellow. Basal knobs of antennae light grayish yellow. Labium light gray. Thoracic shield the same color as the head. A light median line along the length of the prothorax. Individual segments of the body darker posterierly. A dark median line along the dorsal surface of the entire larva. Ventral surface of the larva much lighter, being whitish gray in color.

The larva appears very much like a typical noctuid larva except for the position of the spiracles of the eighth abdominal segment. The spiracles on the other segments of the body occur in the natural place,

but the spiracles of the eighth segment have migrated from the lateral margin to a position on the posterior margin of the dorsal surface, as shown in Plate XLI, 30. The ninth abdominal segment consequently is much smaller, being only about half as thick dorso-ventrally as the other segments. This better adapts the larva to live in its burrow in a plant where an excess of moisture occurs. It is not at all uncommon to find a larva entirely submerged in the water with the exception of these large spiracles, which protrude above the surface of the water. These two spiracles are more than twice as large as the other abdominal spiracles.

The arrangement of the tracheal system in the larva is shown in Plate XLI, 31. It consists of two main longitudinal tubes, which originate from the spiracles of the eighth abdominal segment and extend as far forward as the first thoracic segment, where they are united by a transverse trunk. From this transverse trunk arise the tracheal tubes of the head. Paired spiracles are present on the meso- and metathorax and on the first eight abdominal segments. All of these spiracles are functional except those of the metathorax, which are much reduced and seem almost vestigial. Each of the spiracles, except those on the eighth abdominal segment, are connected with the main tracheal trunk of the body by small tubes, the tubes on the metathoracic segment being reduced to mere threads. Most of the tracheal branches of the body take their origin from the longitudinal trunk, near its junctions with the spiracles. From the thoracic spiracles, only small, branching tubes originate. From the first abdominal spiracle a large tracheal tube originates from the tube joining the spiracles to the longitudinal trunk, and smaller branches spring from the trunk. Segments 2, 3, 4, 5, and 6 of the abdomen each have a pair of large tubes arising from the main trunk just above the spiracles. These tubes branch out into two parts, as shown in Plate XLI, 31. Segment 7 of the abdomen has a number of smaller branches, and segment 8 has a number of still smaller branches in front of the large spiracles.

The pupa (Plate XLI, 23)

Female, average length 32.85 mm., width 7.25 mm., male, length 28.5 mm., width 6.7 mm. Head, thorax, and appendages black. Abdomen dark brown. Frontal prominence very weak. Wings extending back over two-thirds of the fourth abdominal segment. Prothorax about two-fifths of the length of the metathorax. Surface of the head and thorax rugose. Clypeo-labral suture very distinct. Labium distinct, the labial palpi nearly twice as long as labium. Maxillae extending to the posterior margin of

the third abdominal segment. Femur of prothoracic leg not visible. Prothoracic tibia and tarsi prominent, reaching down two-thirds the length of the maxillae. Mesothoracic legs extending to the tips of the maxillae. Metathoracic legs invisible. Antennae reaching almost to the tips of the maxillae. Segments 4, 5, and 6 of the abdomen crossed dorsally by a transverse line of tubercles; the surface in front of the ridge coarsely punctate, but the part of the segment caudad of the ridge very finely punctate. On the ventral surface these transverse ridges occurring on segments 5, 6, and 7. Cremaster about as wide as it is long, somewhat flattened dorso-ventrally, very rugose, and bearing four short setae of equal length. Spiracles on the eighth abdominal segment dorsad. Female with two genital orifices. The peculiar sculpturing of the larva carried over and showing somewhat in the pupa.

The adult (Plate XLI, 26)

Length of body of female, 26 mm. Expanse of wings 54 mm. The original description by Walker (1865 : 438) is as follows:

Cinereous brown. . . . Antennae moderately pectinated in the male, slightly pectinated in the female. . . . Femora and tibia fringed; spurs moderately long. Fore wings with a dark brown oblique stripe, which extends from the base of the interior border to the tip of the wing, and is very diffuse on the outer side: an oblique fusiform pale cinereous ringlet; another ringlet of like shape and hue, longitudinal, nearer the base, much smaller than the first and often obsolete; two submarginal oblique lines of blackish lunules: exterior border almost straight, rather oblique. Hind wings with a black oblique spot in the disk beneath.

Nonagria oblonga Grote

Nonagria oblonga Grote, a moth which also belongs to the family Noctuidae, has been reported by various authors as boring in the stems of *Typha latifolia*. Walton (1908) has described to some extent the habits of the later larval stages and has figured the full-grown larva, the pupa, and the adult. The writer has found the species to be common on *Typha latifolia* near Lawrence, Kansas, and in the following places around Ithaca, New York: Vanishing Brook, Cascadilla Creek, Bool's Back Water, Renwick Marsh, and Michigan Hollow.

Life history and habits

Nonagria oblonga Grote apparently produces only one generation a year.

Egg-laying.— The writer has been unable to find the eggs of this species, although the work of the larvae, from the first instar on, has been observed for three seasons, two seasons around Ithaca and one season in Kansas. The young larvae may be found just as soon as the cat-tail leaves appear above the surface of the ground. In Kansas, on April 20, 1917, when the leaves of the cat-tail were not more than four inches above the surface of the ground, the larvae were found at work in the tips of the leaves.

Although the larvae had evidently just started their work, and more larvae continued to appear during the following days, no eggs could be found on the plants. Again, in Ithaca, on May 20, 1918, first-instar larvae were discovered at work in the tips of the leaves, but no trace of the eggs could be discovered. This suggests the possibility that the females deposit their eggs in the fall on some of the old plants or other objects in the field, and that the species overwinters in the egg stage.

The larva.— The larvae enter the leaf of the cat-tail near the tip and at once begin to work as leaf miners. In their mining they do not restrict their work to the longitudinal channels, as do the larvae of *Arzama obliqua*, but they zigzag back and forth in the leaf, cutting through both the longitudinal and the transverse partitions. They feed on the chlorophyll and on the spongy parenchyma of the plant. The larvae are strictly solitary in their habits; only occasionally do two, or sometimes three, larvae occur in the same mine or even in the same leaf. The characteristic mine produced by the larva is shown in Plate XLII, 37. It is easily distinguished from the mine made by *Arzama obliqua.*

When the larvae are ready for the first molt, they suddenly widen their mine to the outer margins of the leaf, thus producing a narrow transverse mine extending nearly the entire width of the leaf but not severing it completely. This causes the leaf to wither from this point outward to the tip. In this withered part of the leaf the larvae molt, after which they mine downward through the lower, uninjured part. It seems that the natural condition of the leaf, which is very moist, is unfavorable to the molting of these larvae, and it is in order to overcome this excess of moisture that they sever the conducting tissues, thus causing the leaf to dry quickly. In this manner they obtain the required dryness in which to shed their first coat. This allows the larvae to remain under cover, where they are more protected than they would be in the open. The characteristic appearance of such a leaf and the cast skin of one larva in the severed part of the leaf, just above the transverse cut, are shown in Plate XLII, 37.

The larvae of this species do not cease mining after their first molt, and come out of the leaf, as do the larvae of *Arzama obliqua*, but continue as miners in the leaf for some time, often remaining in the leaf through the second, and even through part of the third, instar. Then, however, the larvae crawl away from the upper part of the leaf and seek protection

behind the sheath of the outer leaf, where they feed for a time before they enter the stem and become true stem borers. If the larvae emerge from the leaf soon after the first molt, they usually go down to the sheath of one of the first-formed leaves and there mine in the sheath for some time before entering the stem. Occasionally they feed for a while between two contiguous leaves. The effect of *Nonagria oblonga* Grote is easily recognized on the plant, since the work of the first-instar larva always causes the leaf at first to bend over and wither, and later, after the severed portion has become dry, to break off and fall to the ground. The leaf thus broken at the end, and the presence of the mine, are indicative of the work of these larvae. The writer once found a plant in which five leaves had been cut off by these larvae (Plate XLII, 36).

On entering the stem, the larvae work toward the center, where their borings materially hinder the further growth and development of the plant (Plate XLVII, 70). The presence of the larvae in the stems is indicated by the dried and withered central leaves of the leaf bundle. A plant so affected never heads, because the larva keeps the center tunneled out. The habits of the later larval stages of *N. oblonga* and *Arzama obliqua*, and their effect on the plant, are very similar.

Walton (1908) says of the habits of the larvae: "From all appearances the larva feeds for a time on the sheath of the stem, . . . As it increases in size it bores directly into the succulent central shoot, where it afterward remains until emerging as a mature insect."

When the larvae become full-grown, they transform to the pupal stage in the burrow of the plant. The larva lies with its head upward in the burrow. The exit hole is from two to four inches above the pupa and is carefully plugged up with a combination of frass and plant fibers.

Bird (1902) states that Nonagria has an extremely short pupal stage, from seven to nine days being the record of one brood.

At Ithaca, New York, the writer first found pupae on August 2, 1916. In Kansas the insects mature much earlier. There one larva pupated on June 24, 1917, and emerged on July 5, 1917, the pupal stage covering only eleven days.

The adult.— Around Ithaca the first adults were noticed on August 8, 1916, while in Kansas they were beginning to emerge by the 30th of June. Whether there is a second generation, especially in Kansas where the adults emerge so early, the writer has not been able to ascertain. The

adults failed to mate and lay eggs in captivity. However, no larvae were observed at work on the cat-tails later in the season. Therefore it is likely that if there is a later generation, it occurs on another plant.

Description of the stages

The larva.— The color markings of the larvae (Plate XLVII, 67) vary somewhat in different individuals, but mainly only in the degree of intensity of the colors. They may be described as follows:

General ground color light brown with a slight tinge of flesh color. Head light brown, mottled or speckled with darker brown. Epicranial suture, mandibles, and area just above the clypeus and laterad, darker brown. Six longitudinal, flesh-colored to brownish stripes along the entire length of the body. On each side of the median dorsal line two broad stripes; and laterad to these stripes narrow stripes, located on the lateral margin of the body. Above the spiracles another broad stripe. Below the spiracles, often, another more or less broken line, especially noticeable in the young larvae. Prothoracic shield light brown. At the base of the hairs on the body a dark brown spot. Dorsal surface of the last abdominal segment light brown, speckled with darker spots. Ventral side of the body of a light yellowish color. Length of full-grown larva, from 40 to 50 mm.; width, from 4.5 to 5 mm. Larva cylindrical in shape and not as much flattened as the larva of *Arzama obliqua.*

The pupa (Plates XLII, 33, and XLVII, 71)

Average length 27 mm.; width 7 mm. Color reddish brown, with head, thorax, and cremaster darker brown. Head with a conical projection about 2 mm. long. Wings extending backward over three-fourths of the fourth abdominal segment. Prothorax half as long as the mesothorax. Surfaces of the head and thorax nearly smooth. Anterior margin of labrum sinuate. Labial palpi about two and one-half times as long as the labrum. Maxillae extending about one-sixth of the distance along the fourth abdominal segment. Maxillary palpi present as small triangular pieces. Prothoracic femur visible. Prothoracic legs extending two-thirds the length of the maxillae. Mesothoracic legs reaching a little beyond the tips of the maxillae. Antennae reaching a point half-way between the tips of the mesothoracic legs and the tips of the maxillae. Metathoracic tarsi visible. Abdominal segments 2 to 7, inclusive, dorsally roughened with tubercles, especially prominent on segments 5, 6, and 7. Cremaster somewhat bilobed, with a rough margin bearing four straight setae, two originating underneath, and the other two originating above, laterad to the median line. All these setae equidistant from each other, the middle ones being longer than the outer ones.

The adult.— The adult (Plate XLVII, 68) is of a pale reddish or yellowish color, measuring about 35 millimeters across the extended wings. The original description of the adult, as found in Grote (1882), is as follows:

Male. Pale reddish or yellowish gray, something the color of *Mythimna, Pseudargyria,* Guen. Primaries somewhat oblong, internal angle rounded away; apices softened, costa

a little arched. Eyes naked. Clypeus mucronate. Palpi prominent, concolorous. Markings obsolete. The fine dark linear denticulate t. p. line barely discernable. Stigmata very vaguely indicated by paler shades. Hind wings with a faint mesial black shade band; centrally stained with blackish; fringe and external edge like abdomen and very little paler than the rest of the insect. Beneath pale, with the disk of fore wings blackish; a common blackish extra-mesial shaded line. Minute black discal points. Smaller than *Typhae*.

Arsilonche albovenosa Goeze

Arsilonche albovenosa Goeze is another member of the family Noctuidae. It is found in Canada and in the northern, eastern, and central parts of the United States. It is a general feeder and has been reported on willow, smartweed, buttonbush, grass, and other plants. *Typha latifolia*, the writer believes, is here reported for the first time as a food plant of this species.

Life history and habits

This moth is reported to have two generations a year. The writer, however, has followed it through only one generation at Ithaca, where two adults emerged on August 15.

Egg-laying.— The eggs are deposited in long patches on the surface of the cat-tail leaf, usually ten to fifteen inches from the tip. The eggs overlap one another as shingles do. They lie on the leaf in rows, the number of rows varying from three to seven, and the rows overlapping one another as well as the individual eggs in each row. The number of eggs in one patch ranges from 60 to 161.

As the egg develops, it becomes much darker, turning very dark just before the larva emerges.

The larva.— Immediately after hatching, the larva devours the empty shell and then begins to feed on the surface of the Typha leaf, where it scrapes off the chlorophyll. As the larva grows and feeds more voraciously, it usually migrates to the end of the leaf, where it eats off the tip of the leaf or devours chunks out of the edge of the leaf, as shown in Plate XLVI, 62.

When the larva has attained its full growth, it ties two cat-tail leaves together, and between them spins a tough cocoon in which it pupates. Two larvae pupated in the laboratory, under the author's observation, on July 23, 1916, and two others on July 25, 1916. The former both emerged on August 15, 1916. This apparently indicates the length of the pupal stage to be nineteen days.

Description of the stages

The egg (Plate XLVI, 61)

Flat; saucer-like or shell-like in shape, and grayish white in color. Diameter, as seen from the top, varying from 0.89 to 1 mm.; thickness of egg about 0.2. Sculpturing very pretty, micropyle in center of dorsal surface consisting of a dot with a rosette of elongate cells around it. Radiating from the rosette to the margin of the egg, about 45 small ridges, indented transversely by small, rounded depressions.

The larva.— The first-instar larva, within twenty-four hours after hatching, is described as follows:

Length 2 mm. Entire head jet black; thoracic shield dark brown; meso- and metathorax light gray with dark tubercles. Segments 1, 4, 5, and 8 of the abdomen dark brown, with gray tubercles. The other segments of the abdomen light yellow, with gray tubercles. From these gray tubercles originate long hairs.

Beutenmüller (1901) gives the following description of the full-grown larva (Plate XLVI, 62):

Head black, with an inverted V mark on the face, two white stripes on top, and mottled with white at the sides. Body black, two yellow lines on each side of the back and one on each side below the spiracles. The body is also mottled with confluent striae, but less so on the dorsum. Warts orange with light and dark bristles; along the extreme sides a row of orange spots. Underside pale whitish. Length 40–45 mm.

The pupa (Plate XLVI, 63)

Length 18 mm., width, 5 mm. General color dark brown. Wings extending as far back as the fourth abdominal segment. Front of the head with two rounded, rugose ridges running up and down. Clypeo-labral suture very distinct. The front margin of the labrum rounded. Labial palpi three times as long as the undivided labium. Maxillae extending down to the beginning of the third abdominal segment. Prothoracic femur visible and the prothoracic tibia and tarsi extending down almost to the tips of the maxillae. Mesothoracic legs extending to the middle of the fourth abdominal segment. Antennae just failing to reach the tips of the mesothoracic legs. Metathoracic tarsi plainly visible. Ventral surface of segments 5, 6, and 7 finely granulate anteriorly, posteriorly finely punctate. The other segments smooth. On the dorsal surface, the metathorax and the first seven abdominal segments very roughly tuberculate. Cremaster broader than it is long and bearing from 40 to 50 short, straight spines.

The adult.— The adult (Plate XLVI, 64) is described as follows by Beutenmüller (1901): "Fore wings white, and more or less heavily marked with fawn brown streaks between the veins, giving the insect a very characteristic appearance. Hind wings and body white. Expanse, 34-45 mm."

Archips obsoletana Walk.

Archips obsoletana Walk. is a moth belonging to the family Tortricidae. This insect has been reported from the Atlantic states and from Illinois. The author has found it in Kansas and in New York. Slingerland (1901) suggested "the obsolete banded strawberry leaf-roller" as a common name for the insect. *Archips obsoletana* Walk., although it lives on various host plants, prefers those which grow in moist situations, and is here reported on *Typha latifolia.*

Life history and habits

The habits of this insect as a leaf-roller on strawberry have been studied rather carefully by Slingerland (1901). According to his report, there are three generations a year in New York. It is not known in what stage the insect passes the winter.

Egg-laying.—The eggs have not been observed in nature. In the laboratory, they were deposited in a large mass on the side of the glass cage.

The larvae.— The writer's observations on the habits of the larvae of this species have been restricted to those specimens found on *Typha latifolia.* The larvae and their work on cat-tail were first noticed on some cat-tail heads from Lawrence, Kansas, sent to the author by Dr. H. B. Hungerford and received at Ithaca on July 17, 1916. A number of the heads showed the effects of the work of the larvae of *Archips obsoletana.* On August 12, 1916, larvae of this species were also found at work on the heads of cat-tail plants in the McLean Bogs. One pupa was also discovered at this time.

The larva works on the immature heads of the cat-tail, feeding on the tender styles of the pistillate flowers and sometimes eating off the tops of the developing ovules (Plate XLVII, 69 and 72). The stigmas are not eaten; instead they are lined underneath with a thin, but closely woven, layer of silk. This silk layer, together with the stigmas on top, forms a protective covering over the larva. When this covering is torn loose, the larva quickly repairs it.

In the laboratory, the larvae at times left the heads and fed on the leaves of the cat-tail; but they always provided themselves with a protected place, either by tying two leaves together or by spinning a silken tube between a leaf and the side of the glass cage. In this tube the larva remained, never leaving it entirely but always keeping the tip of the

abdomen covered and protruding the head to feed. As the larva fed downward, it lengthened this silken tube. In the field, the author has not observed the larvae feeding anywhere on the plant except on the head.

When the larva becomes full-grown, it goes to the top of the head, to which it then ties a leaf in order to form a place in which to spin its cocoon for pupation. The silk used to tie the leaf to the head is covered with a mixture of frass and the remains of the staminate flowers. If a leaf is not within reach of the larva, the cocoon is made on top of the head, near the rachis, and covered with the remains of the staminate flowers. After pupation, the wind and rain soon tear off the covering made by the larva and the head has then the appearance of having been shaved in patches (Plate XLVII, 73).

Description of the stages

The egg.— Slingerland (1901) describes the egg somewhat as follows:

Thin, oval, light lemon yellow, overlapping each other not unlike the shingles of a house. Shell is finely reticulated, the micropyle showing plainly at one end.

The larva.— The larva may be described as follows:

Olive green, with a light brown head and thoracic shield, both marked with black; the body sparsely clothed with light-colored hairs arising from pale, roughened tubercles. The newly hatched caterpillar light yellow, with a brown head. Length of full-grown larva, about 17 mm. (Plate XLVII, 76).

The pupa.— The pupa is shown in Plate XLVII, 74. The following description applies to the female.

Length, including cremaster, 12 mm.; width, measured across the wings, 3.8 mm. General color reddish brown, the wings being somewhat lighter-colored than the rest of the body. Wings reaching back as far as the middle of the fourth abdominal segment. Thoracic region much enlarged, the appendages forming a distinct salient. Front of the head with an inverted Y ridge, as viewed from the cephalic aspect. A transverse ridge at the base of this Y. Clypeus and labrum prominent, and the clypeo-labral suture distinct. Labium clearly visible. Labial palpi one-fourth as long as maxillae. Maxillae extending half way to the tips of the wings. Maxillary palpi elongate and triangular, reaching to the pro-lateral angles of the maxillae. Coxae of mesothoracic legs visible below the maxillae and the femora. Femur and tibia of prothoracic legs large. Mesothoracic legs extending below the tips of the antennae. Antennae shorter than the wings by 0.8 mm. Metathoracic tarsi visible beyond the tips of metathoracic legs and antennae. Genital orifice double. Cremaster slender, tapering, longer than it is broad, and bearing eight stout, curved setae, four extending from the apex and two on each side. Setae of body long and prominent. On the dorsal surface, the first abdominal segment smooth. Segments 2 to 8, inclusive, each having two

transverse rows of strong spines, most prominent on segments 4, 5, 6, and 7. A few spines present on the ninth abdominal segment.

The adult.— The following description of the adult (Plate XLVII, 75) is quoted from Slingerland (1901):

General color varies from a wood-brown through cinnamon to russet; the hind wings and all four wings beneath are of a lighter yellowish-brown color. Many fine, wavy, transverse, dark brown lines occur on the front wings, showing more distinctly in the male. And extending obliquely across these wings is a broad, dark brown band, more or less obsolete in the middle, and there is a subapical spot of the same color on each front wing.

Lymnaecia phragmitella Staint.

Lymnaecia phragmitella Staint. is a little moth belonging to the family Tineidae. Without question, this is the most common and the most abundant of the insects infesting the cat-tail. In distribution it is world-wide. It is found in England, central and southern Europe, northern Africa, Australia, New Zealand, and the United States. Its host plants are *Typha latifolia* and *T. angustifolia*. The writer has invariably found that the majority of Typha plants in any patch are infested by this insect.

Life history and habits

The larva.— Regarding the larvae of this species, Stainton (1870) wrote:

If we visit a boggy piece of ground where *Typha latifolia* grows, we shall find that some of the thick club-like heads of that plant exhibit a curious, tattered and frayed appearance; if the period of our observation be autumn, we shall find on examining amongst the soft downy interior of the fertile catkin some small larvae; if we seek at the end of winter or in early spring, we shall find the same larvae, nearly full fed, about five lines long; and if these larvae are rather broad and flat, of a yellowish-white, with broad darker lines, we need not hesitate to pronounce them the larvae of *Laverna phragmitella*.

The larvae restrict their work to the head of the plant, except occasionally when they bore into the stem to transform (Plate XLII, 35). The young larvae feed on the tender styles of the pistillate flowers, but as these grow larger and become dry, the larvae move farther inward and eat the seeds of the plant. As cold weather approaches, they migrate still farther inward, and finally locate near the rachis of the flower spike, where they often eat away the basal part of the little stalks which bear the seeds. The larvae spin an abundance of silk with which they tie the down, or pappus, together, thus keeping it from being torn off or blown away.

The cat-tail heads which are infested by these larvae present a striking appearance. The silk spun by the larvae holds the downy material together and does not allow the seeds to escape, but the heads fluff out

greatly and become twice or three times their natural diameter. Two heads, one heavily infested with the larvae of *L. phragmitella*, and the other uninfested, are shown in Plate XLV, 59. This is the appearance of the heads in the fall. During the winter and spring the uninfested heads lose all their seeds so that only the rachis remains, but the infested heads retain their seeds in the fluffy condition just described till the following summer, when the heads finally drop to the ground. A field in which the majority of the heads are heavily infested is shown in Plate XLIX, 84. This photograph was taken in July, just about the time that the new heads were forming. In the old heads, as well as in the newly formed ones, these larvae were present.

The larvae overwinter in the half-grown stage in the head of the plant, the fluffy material of the fruiting spike being their protection.

In the latter part of May or early June the larvae attain their full growth. Then, in the midst of the downy material, the larvae spin their thin, tough, white cocoons and transform to the pupal stage. Many of the larvae, leaving the heads, go down and bore into the stem of the cat-tail plant, forming burrows which they line with silk; and there they pupate.

In the laboratory, larvae were placed in vials containing little bunches of seeds from the head of Typha. The larvae spun cocoons in the vials and pupated. Some of the larvae bored into the corks, lined the tunnels with a little silk, and then transformed.

The average pupal stage lasts 29.4 days. This was ascertained from data on five individuals in the laboratory, as shown in table 7. Cocoons

TABLE 7. DETERMINATION OF THE PUPATION PERIOD OF LYMNAECIA PHRAGMITELLA STAIN.

Specimen	Date of pupation	Date of emergence	Length of pupal period (days)
1	June 4	July 1	27
2	June 6	.....	..
3	May 30	July 1	32
4	May 31	July 3	33
5	June 5	July 6	31
6	June 4	June 28	24
Average	.....	.....	29.4

and pupae, as they were removed from the pappus of the head of a Typha plant, are shown in Plate XLVIII, 82.

The adult.— The first adults were observed to emerge in the laboratory on June 8, 1916, and the maximum emergence occurred between June 25 and June 30. In the spring of 1918, the moths first appeared in the laboratory on June 10. Immediately after emergence the adult moths often rest on the cat-tail heads, as shown in Plate XLIX, 85. Stainton (1870) speaks of the adult as follows:

If in July we visit a locality in which the *Typha latifolia* grows we may probably find towards evening some small grayish-ochreous moths, with the anterior wings rather streaked with brownish towards the apex, and with two dark brown spots ringed with white on the disc; these would no doubt be the perfect insects of *Laverna Phragmitella*.

Description of the stages

The larva (Plate XLII, 32)

Length from 10 to 12 mm., width 2.5 mm. General ground color yellowish white. Ventral side entirely white, with the exception of the brownish, chitinized legs and prolegs. Dorsal surface with 5 longitudinal brown stripes. The median stripe rather narrow; the next stripe, on each side of the median line, wide and somewhat lighter in color; the stripes on the lateral margin, above the spiracles, more or less broken into blotches. Head light yellow, blotched with brown. Epicranial suture dark brown. Posterior part of the head dark brown. Mandibles and labrum dark. Prothorax mottled with dark brown. The last abdominal segment dotted with dark brown spots, as shown in Plate XLII, 32.

The pupa (Plate XLII, 34)

Length 9–10 mm., width 2.1–2.3 mm. General color yellowish brown. Head with a blunt, rounded projection. Wings reaching to the middle of the sixth abdominal segment. Front of clypeal suture faint. Labrum with outer margin rounded. Labium not visible. Maxillae broad at the base and much narrower at the proximal half. Maxillary palpi present as small triangular pieces. Prothoracic legs extending two-thirds the length of the maxillae. Mesothoracic legs not reaching quite to the tips of the maxillae. Antennae very slender, reaching the tips of the wings, and contiguous all the way to the tip. Metathoracic legs invisible. Rudimentary prolegs visible on the sixth segment. No definite sculpturing on the body. On the dorso-caudad surface of the last abdominal segment, eight hooked setae, arranged in groups of four. In each group three setae in a straight transverse line, but the fourth seta just cephalad to the middle one of the group. Cremaster undeveloped.

The adult.— The length of the adult, with wings folded, is from 10 to 12 mm. Stainton (1870) gives the following description of the adult:

Head pale brownish-ochreous, face paler. . . Antennae pale grayish-ochreous, spotted with dark fuscous. . . Anterior wings pale brownish-ochreous, the costa beyond the

middle paler; on the disc, nearly in the middle, is an elongate dark brown spot surrounded by white, and in a line with it at the end of the discoidal cell is another similar spot: a brownish streak frequently connects the two, and the entire apical portion of the wing is more or less streaked with brown. . . . Posterior wings pale gray, with grayish-ochreous cilia.

Dicymolomia julianalis Walk.

Dicymolomia julianalis Walk. is a member of the family Pyralidae. It is found throughout the southern part of the United States. Ithaca is probably near its northern limit. Its host plant is *Typha latifolia.*

Life history and habits

Dicymolomia julianalis Walk. has but one generation a year. It passes the winter in the half-grown larval stage. The habits of this insect are very similar to those of *Lymnaecia phragmitella.*

Egg-laying.— The eggs of *D. julianalis* are placed in the heads of the cat-tail, being inserted singly in the down, or pappus, of the seed. They are fastened to the pappus at about the level of the kernel of the seed. The eggs were first found on July 25, 1918, at which time they were rather common. It was not at all difficult to locate them, once it had been discovered where to look for them. The period of egg-laying has not been carefully determined, but apparently there were no eggs laid before the middle of July and none after August 10. The eggs are placed in the heads of the cat-tail with the blunt, or anterior, end outward. Several eggs are shown in the cross section of a head of *Typha latifolia,* in Plate XLIII, 45.

On July 25, 1916, the writer watched one of these eggs hatch. The larva lay in the egg, stretched to its full length, and could be seen moving back and forth inside the egg shell. It ate its way through the egg shell and escaped (Plate XLIII, 46). When about half of its body was out of the shell, the larva gained a foothold on the pappus and pulled itself the rest of the way out of the shell. The larva does not devour the empty shell, but at once buries itself in the head of the plant, where it eats the tender styles of the pistillate flowers. The empty shell remains attached to the pappus. The time from the moment that the larva actually began to eat through the egg-shell till it was freed was about twenty-five minutes.

The larva.— *D. julianalis* spends its entire larval period in the head of the cat-tail, obtaining its food, first from the styles of the pistillate

flowers, and later from the seeds and the dried-up parts of the flower. As soon as hatched, the larva begins to feed on the styles, leaving the stigmas to form a sort of covering over itself. These severed stigmas are spun together with a little silk and thus held in place. The larval habits of both *Lymnaecia phragmitella* and *D. julianalis* are very similar in their early stages. As the cat-tail heads become more mature, and the larvae grow larger, they enter deeper into the head, and their presence is not so readily detected as when they are working near the outer surface where the little raised patches of fluffy material they produce are easily seen. The appearance of a head of Typha within a week after the larvae had hatched and entered the head is shown in Plate XLIX, 86. As in the case of *Lymnaecia phragmitella*, the seeds are kept from scattering, by being tied together with silk woven by the larva. Neither wind nor rain is able to tear apart the heads so protected. Accordingly they form a good shelter for the larvae during the winter. The larvae of *D. julianalis* bore into the axis of the flower spike and there spend the winter in the half or two-thirds-grown stage. The rachis, with the characteristic tunneling of the larvae, is shown in Plate XLIII, 42 and 43. These tunnels are later lined with a little silk and in them the larvae construct tightly-woven cocoons in which they transform to the pupal stage. Many of the larvae, however, remain in the fluffy material in the heads to spin their cocoons and pupate. Pupation begins about the first of June. The adults emerge during the latter part of June and the first part of July.

During the spring of 1916 the author did not find any dead larvae in the heads of the cat-tail; but in the spring of 1918 all the larvae of this species which he observed were dead, evidently having been killed by the severe cold of that winter. At that time even the larvae in tunnels of the axes of the heads were dead. This was not true of the larvae of *Lymnaecia phragmitella*, however.

Description of the stages

The egg

Elongate oval, tapering considerably toward the posterior end and rather blunt at the anterior end (Plate XLIII, 38). Very long in proportion to its width, measuring 1 mm. in length and 0.219 mm. at its greatest diameter. Color of egg white, with a slight bluish tinge in refracted light. Sculpturing rather faint, consisting of fine, more or less hexagonal reticulations (Plate XLIII, 39, drawn with the camera lucida).

The larva.— The larva of the first instar is shown in Plate XLIII, 40. The following description is taken from a larva about thirty minutes after its emergence from the egg:

Length 1.19 mm., greatest width 0.28 mm. General color light pinkish or flesh color. Head and thoracic shield mottled with darker brown, restricted in the thoracic shield to the posterior part. A dark mottled area on the dorsal surface of the last abdominal segment also.

The full-grown larva (Plate XLIII, 41) is described thus:

Length from 7 to 10 mm.; about 2 mm. at its greatest width. Much flattened, and in general shape much like *Lymnaecia phragmitella*. General color flesh color. No special markings on the body except, as in the first instar, on the dorsal surface of the first thoracic segment and on the last abdominal segment. Head dark brown, with darker blotches near the outer margin. Epicranial suture very dark brown. Prothoracic shield dark brown, slightly lighter than the head, with two oblique oval spots near the lateral margin, the shield being mottled near the posterior margin. Dorsal surface of the last abdominal segment mottled with brownish patches or spots, as shown in Plate XLIII, 41. Larva easily distinguished from that of *Lymnaecia phragmitella* in that it does not possess the five longitudinal stripes on the dorsal surface of the body.

The pupa (Plate XLIII, 44)

Length 7–8 mm., width 2.9–3 mm. General color yellowish brown to dark brown. Front of head not visible from the ventral aspect. Clypeo-labral suture distinct. Labrum with an emargination and very small, appearing somewhat like an arrow head. Two long hairs on the clypeus. Wings extending two-thirds across the fourth abdominal segment. Maxillae extending to the wing tips. Maxillary palpi absent. Prothoracic femora visible. Prothoracic leg extending two-thirds the length of the maxillae. Mesothoracic legs reaching to the tips of the wings. Antennae reaching to a point halfway between the tip of the prothoracic leg and the tips of the maxillae. Metathoracic legs not visible. Cremaster subquadrate, nearly smooth, with six equally long, hooked spines arranged in groups of threes on the outer angle of the cremaster. Rudiments of prolegs on segments 5 and 6 of the abdomen. General surface of the body smooth.

The adult.— The adult female, shown in Plate XLVIII, 81, measures 6 mm. in length and has a wing expanse of 18 mm. Walker (1859) describes the adult as follows:

Whitish, slightly marked with ferruginous. . . Antennae stout, submoniliform. Abdomen with brownish speckles. . . Legs stout. . . Fore wings with two reddish bands; the first exterior; the second marginal; the intermediate part with blackish speckles, which are somewhat confluent by the bands.

COLEOPTERA

Calendra pertinax Oliv.[4]

Calendra pertinax Oliv. is a beetle belonging to the family Calandridae. Blatchley and Leng (1916) state that *Calendra pertinax* "ranges from New England and Canada to Michigan and Utah, south to Florida." Satterthwait (1920) reports this species from the following states: Indiana, Missouri, Maryland, and New York. The author has collected and reared it in Lawrence, Kansas, and in Ithaca, New York. A variety of *pertinax*, called *typhae* Chittendon, has been reared from the roots of *Typha latifolia* in California. The known host plants of *C. pertinax* are *Typha latifolia*, *Acorus calamus*, corn (*Zea mays*), and *Sparganium* sp. The writer has found *C. pertinax* in *Typha latifolia* and in *Sparganium* sp.

Life history and habits

The weevil is found to be most abundant in Typha patches where the plants grow in sod or grassy soil. This has been found to be true in New York as well as in Kansas. In the wet, grassy places along the railroad tracks south of Ithaca, where Typha grows intermingled with various species of grasses, the larvae were found to be most numerous. In some of these patches nearly every plant was infested. However, the weevil was found also in the larger cat-tail patches of Renwick Marsh around the biological field station.

Egg-laying.— The eggs are inserted into the outer sheath at the base of the plant, very near the surface of the ground. No females were actually observed in the act of ovipositing, but the newly laid eggs were always found with the end protruding from a little slit in the sheath (Plate XL, 17). In very wet places it is likely that the eggs are placed above the surface of the water, but the writer observed them only on cat-tails growing in a rather dry situation.

The period of egg-laying has not been fully determined. Eggs were first found in Kansas on June 28, 1917. At that time, however, first- and second-instar larvae also were found in the plants, so that egg-laying must have started some time before, probably as early as the latter part of May. Eggs were found in the stems as late as July 17, when the

[4] Determined by Dr. E. C. Van Dyke.

observations had to be discontinued. The period of egg-laying is therefore spread over a number of weeks.

The larva.— In the laboratory, the larvae were placed in tin salve boxes which had been partly filled with sterilized sand and moistened with boiled water. A little excavation was made at one end of a fresh piece of the rhizome of cat-tail, and in this the larva was placed and left to feed. Such pieces of rhizome, two or three inches long, remained fresh from three to five days. As the larva became older and needed more food, these pieces of rhizome had to be replaced more often. By splitting the piece open, excavating a little hole in the center for the larva, and then binding the pieces together again with rubber bands, observations could be made from day to day without unduly disturbing the larva.

As soon as the larvae are hatched, they begin to bore directly into the stem, working toward the center, and thence downward toward the crown, and from there into the central axis of the rhizome (Plate XL, 19). Like the other borers of the cat-tail, this larva at once seeks the central part of the plant, where the tissue is most tender and succulent. However, the weevils seem to have a special preference for starchy food, and for this reason they work downward to the rhizome, the core of which is composed mainly of starch (Plate XLV, 60). In rearing the larvae, it was found that they would not eat any other part of the rhizome except the starchy core. As many as seven larvae have been found in a single plant. In one instance they were all working at the crown and as a result had nearly cut off the plant.

The affected plants present a somewhat stunted appearance. Sometimes the central leaves die and the plant fails to head out. The tunneled rhizomes shrivel up considerably and often darken decidedly.

The larvae grow very rapidly, and the time from hatching to the pupal stage averages about three weeks. When the larva has become fully grown, it prepares an oblong pupal cell in the stalk of the plant, from one to three inches above the ground (Plate XLVIII, 80). The pupal cell is made of partly masticated pieces of the stalk, with which the burrow is plugged above and below. In the laboratory some of the larvae pupated in their burrows in the rhizome, while others, that were reared in plants growing in flower pots, tunneled through the soil to the bottom of the pot and there made a smooth, oblong, unlined, earthen cell in which they transformed. The reason for their going down into the soil appeared to be a

desire for a moist place in which to pupate. The plants in the pots had dried up completely, and the soil, too, was quite dry, so that in order to find a moist place the larvae were forced to go to the bottom of the pot.

The length of the pupal stage seems to vary considerably. Eight pupae were kept under observation, and the results are given in table 8:

TABLE 8. LENGTH OF PUPAL STAGE OF CALENDRA PERTINAX OLIV.*

Specimen	Date of pupation	Date of emergence	Length of stage (days)
1	July 15, 1917	July 24, 1917	9
2	July 15, 1917	July 22, 1917	7
3	July 19, 1917	.....	Died
4	July 21, 1917	July 27, 1917	6
5	July 27, 1917	.....	Put in preservative
6	July 26, 1917	August 8, 1917	13
7	July 29, 1917	August 11, 1917	13
8	July 29, 1917	August 11, 1917	13
Average			10.16

* The data on the first six pupae were determined for the writer by Dr. P. B. Lawson, of Lawrence, Kansas. The last two pupae were observed by the author himself.

Description of the stages

The egg (Plate XL, 16)

Average length 2.15 mm., average greatest width 0.85 mm. Elongate oval, scarcely subreniform-elliptical. Color almost pure white. No distinct marking or sculpturing. As the time of hatching approaches, turning yellowish, and becoming quite dark just before the larva emerges.

The larva (Plate XLVIII, 77)

Color dirty white. Head yellowish brown. Epicranial suture distinct. On each side of the epicranial suture a light line starting indistinctly at the vertex and running obliquely to the frontal suture. Mandibles very dark brown, almost black. Front of head darker near the fronto-clypeal suture. Clypeus light brown. Labrum with two curving sulci which divide it into three subequal parts. On the labrum four prominent hairs and a number of marginal hairs. Thoracic segment distinct. Prothorax with a yellowish, chitinized shield. Spiracles of prothorax large, oblong, and nearly twice as large as the other spiracles. Segments 4, 5, and 6 of the abdomen greatly enlarged. Spiracles located on the dorsal surface. Length of larva, in its curled-up position, about 13 mm.; when straightened out, about 16–17 mm.; greatest diameter 7 mm.

The pupa.— The pupa is shown in Plate XLVIII, 79. The size of the pupae varies considerably. The average of the measurements of six pupae (table 9) showed the average length to be 14.2 millimeters and the width, taken across the prothorax, 5.76 millimeters.

TABLE 9. MEASUREMENTS OF THE PUPA OF CALENDRA PERTINAX OLIV.

Specimen	Length (millimeters)	Width (millimeters)
1	15.8	7.0
2	13.2	5.2
3	12.5	4.8
4	15.4	6.3
5	14.8	5.8
6	13.5	5.5
Average	14.2	5.76

The pupa is large, naked, and dirty white in color. It may be described as follows:

From the dorsal view: Head almost or entirely concealed by the prothorax. Prothorax a little longer than the meso- and metathorax combined. Eight spines on the surface of the prothorax, arranged in pairs, near the four corners of the subrectangular dorsum. Mesothorax terminating in a triangular lobe, without spines or setae. Metathorax with two prominent setae. On each of first six abdominal segments a transverse row of setae arranged as follows: segment 1, with a group of three setae on each side of the median line and one laterally just above the spiracle; segments 2 to 6, inclusive, with the same arrangement except that the groups laterad of the median line have four setae; segment 7 with one seta on the lateral margin; segment 8 with stout spines, arranged in groups of fours, on the posterior margin.

From the ventral view: Rostrum stout, reaching to the prothoracic tarsi. One pair of spines at the base of rostrum and another pair in line with the base of the antennae. Antennae elbowed and reaching almost to the tips of the femora. Each femur with a stout spine near the distal end. Wings reaching to the ends of the hind femora. On the eight abdominal segments, in each of the outer two apices, eight spines, arranged in groups of fours.

The adult.— Blatchley and Leng (1916) describe the adult (Plate XLVIII, 78) as follows:

Elongate-oval. Black or reddish-black, shining, the interspaces of thorax and flat alternate intervals of elytra covered with a dirty white coating. Beak as in key, three-fourths the length of the thorax, finely and sparsely punctate, foveate and finely grooved above at base. Thorax longer than wide, foveate and finely constricted; vittae entire, the median one widest at middle, narrowed before and behind; lateral ones with edges sinuous, branched as described

above; interspaces and sides of disc coarsely punctate. Elytra broadest at humeri, sides feebly converging to apical fourth, then more strongly to the rounded apex; striae with rather coarse, regular punctures; the broader and more convex intervals somewhat interrupted, minutely and sparsely punctate. Length 11–15 mm.

Notaris punctiċollis Lec.[5]

According to Blatchley and Leng (1916), *Notaris puncticollis* Lec. (Plate XLVIII, 83) ranges from Newfoundland and Quebec to Minnesota and as far south as the Ohio River. The host plants reported for this species are cabbage, *Peltandra virginica*, and *Typha latifolia*. Webster (1893), writing of *Notaris puncticollis*, says:

> In Wayne County, Ohio, a field of this swamp land was underdrained last year, and last January was plowed; no further cultivation being given it until late spring, when it was prepared and planted to cabbage, about 50,000 in number, set late in June. These have been attacked and many of them destroyed by the adults of two species of Rhynchophora (*Listronotus appendiculatus* Boh, and *Erycus puncticollis* Lec.). The former is supposed to be the chief depredator, though I myself saw the latter attacking the plants. First, great cavities are gouged out of the stems of the young plants, and later the base of the larger leaves are attacked from beneath. . . . . It is not unlikely that one and perhaps both of these species breed in Sagittaria, though I have some reasons for suspecting that the Erycus may breed in the common *Typha latifolia* or cat-tail.

On August 19, 1915, at the field station in Renwick Marsh, W. A. Hoffman found the adult of *Notaris puncticollis* Lec. in the burrow in the stem of Typha. The burrow appeared very much the same as that of *Calendra pertinax*. The writer, however, has not been able to find this species during the course of his studies.

HEMIPTERA

Ischnorrhynchus resedae Panz.[6]

Ischnorrhynchus resedae Panz. is an insect belonging to the family Lygaeidae. It is of general distribution, being reported from Europe, Asia, Central America, Mexico, Canada, and the United States. Among its host plants are included birch, conifer, heath, arbutus, *Typha latifolia*, and *T. angustifolia*. The two species of Typha are here reported for the first time.

Life history and habits

Egg-laying.— The eggs are laid in the spring, during May and June. They are deposited singly in the pappus of the old cat-tail heads of the

[5] Determined by C. W. Leng.
[6] Determined by Dr. H. H. Knight.

previous year. They are attached either to the seeds or to the pappus. When the egg hatches, the nymph either opens the cap or breaks through the egg shell, bursting it near the top.

The nymphs.— The various nymphal stages and the adults were first observed on the overwintering cat-tail heads in the summer of 1916. It was at first assumed that they were merely accidentally present on the cat-tail heads, but closer examination revealed that the bugs were feeding on the dry seeds of the heads.

The nymphs obtain their nourishment by thrusting the stylets of their beaks into the dry seeds (Plate XLIV, 53 and 55). During feeding, the long labium is often folded back under the body. In just what manner the bugs are able to extract nourishment from the dry seeds the author has not been able to determine. When crushed on the slide and examined under the microscope, the seeds show very little moisture. It is very probable that the insects secrete a fluid which dissolves or predigests the dry food material before it is taken into the body. The author has succeeded in rearing nymphs to the adult stage on these dry heads of cat-tail alone with no other food available. When placed on the green leaves of the cat-tail, the nymphs insert their beaks and feed. They are easily disturbed while feeding on the seeds in the laboratory. At the slightest provocation they rise up on their hind legs, quickly extract their stylets, and, by means of their front legs, stroke the stylets back into the labium. The labium is then folded into place and the nymph retreats to some sheltered place.

The adult.— Adults were found mating in May and June. The female inserts her ovipositor into the male and copulation lasts from six to nine minutes. Mating is repeated a number of times at intervals of from five to ten minutes.

Description of the stages

The egg (Plate XLIV, 47)

Length 0.93 mm. to 1 mm., greatest diameter 0.29–0.30 mm. Egg elongate oval in shape, tapering considerably at the posterior end, and closed by a cap at the anterior end. This cap with a cone-shaped protuberance in the center and surrounded by a circle of hooked spines. The upper two-fifths of the egg finely reticulated; the lower three-fifths with longitudinal wavy and branching ridges. Color lemon yellow at first, turning bright red before the nymph emerges. Empty egg shell white. The egg closely resembling the seed of cat-tail, both possessing caps and very similar markings on the surface.

The first-stage nymph (Plate XLIV, 48)

Length 0.857 mm.; greatest width, across wing pads, 0.280 mm. Length of antenna 0.428 mm. When first emerging from the egg, the general color of the nymph bright red. Eyes carmine red. Abdomen, vertex of head, and lateral margins of the body, of a darker color than the rest of the body. Thorax, front of head, antennae, and legs, of a light yellowish color. Several hours after hatching, nymph of a different appearance: Head, thorax, and tip of the abdomen very dark red, almost brown. Abdomen carmine, mottled with yellow. Legs and antennae greenish yellow, the antennae lighter at the joints. The epicranial suture and the median dorsal thoracic line lighter in color.

The second-stage nymph (Plate XLIV, 51)

Length 1.5 mm.; greatest width, across wing pads, 0.368 mm. Length of antenna 0.575 mm. General color carmine red. Head and thorax dark reddish brown. Intermixed with the red color of the abdomen, many yellowish blotches. Antennae dark red, lighter at the joints. Rostrum somewhat lighter than the rest of the head. Epicranial suture and median thoracic line pale. First thoracic segment uniformly dark; in the second segment the dark color restricted to two rectangular patches; in the third segment the darker color present in two transverse lines. The dorsal glands showing as short, brown, transverse lines between the abdominal segments 3 and 4, 4 and 5, and 5 and 6.

The third-stage nymph (Plate XLIV, 50)

Length 2.08 mm.; greatest width, across wing pads, 0.598 mm. Length of antennae 0.69 mm. General color a little darker than in the preceding stage. Head uniformly dark brown, except for the lighter epicranial suture and a lighter spot on the rostrum. Head and thorax covered with faint white pile. In this stage the pro- and mesothorax uniformly dark brown, with the dark patches on the metathorax a little wider than in the preceding stage. The light median line on the thorax present as in the previous stages. The mottled appearance of the red and yellow color of the abdomen more pronounced in this stage. Dorsal glands more plainly visible. Wing pads just beginning to show. Entire body more hairy than in preceding stages.

The fourth-stage nymph (Plate XLIV, 49)

Length 2.71 mm.; greatest width, across wing pads, 0.989 mm. Length of antennae 1.04 mm. Color of head and thorax dark brown. Epicranial suture and median dorsal line of thorax light red. Rostrum of head with a short black longitudinal line on each side. Eyes carmine red. Antennae slightly lighter than head and thorax, much lighter at the joints. Dorsum of prothorax on each side with a blackish, triangular, transverse spot, as shown in Plate XLIV, 49. Wing pads extending 5 mm. beyond the posterior margin of the mesothorax. The mottled color of the abdomen much as in the preceding stage. The white pile on the head and thorax thicker and more plainly visible than in preceding stages. Dorsal glands as in third stage.

The fifth-stage nymph (Plate XLIV, 54)

Length 3.35 mm.; greatest width, across wing pads, 1.61 mm. Length of antenna 1.38 mm. The general color similar to that of the previous stage, but the head and thorax now distinctly patterned. Epicranial suture as in previous stages. The part of the head back of the epicranial suture uniformly dark red. Rostrum yellowish with brown lines on each side, which meet behind the rostrum and then diverge outward until they join the brownish border inside the epicranial suture, thus producing on the head four yellowish patches separated by the brown lines in the shape of the letter X. Prothorax dark brown, punctate with circular yellow spots. From these spots, short white hairs arising. Transverse dark bands on the prothorax, as indicated in Plate XLIV, 54. Rest of thorax, including wing pads, dark brown. The surfaces of meso- and metathorax and the wing pads punctate with yellowish spots, less numerous than those on the prothorax, however. The bases of the wing pads indicated by light-colored, diagonal lines. The margin of the entire thorax and wng pads of a blackish brown color. Wing pads reaching to about the middle of the third abdominal segment. Abdomen colored much as in the preceding stage.

The adult (Plate XLIV, 52)

Female, length 5.4 mm.; greatest width, across the prothorax, 1.5 to 1.6 mm. Length of antenna 1.75 to 1.85 mm. General color dark brownish red. Posterior margin of head and area around eyes and ocelli black. Sides of rostrum black. Basal segment of antennae black, second and third segments of antennae yellowish brown with fuscous at the bases and apices, and the fourth segment dark red. Head and thorax thickly covered with dark punctures. Pronotum with two wavy transverse dark bands near the anterior margin. Corium pale yellowish brown with two black spots on the disk and four black spots on the inner lower margin. Legs reddish brown. Apical segments of tarsi black. Body covered with a very fine white pile. Male slightly smaller than female.

Siphocoryne nymphaeae Linn.[7]

Siphocoryne nymphaeae Linn., the reddish brown plum aphis, is found in numbers on cat-tail during the spring and summer. This species also uses other water plants as its summer hosts, such as Nymphaea, Potamogeton, and others. The aphids are found on the surfaces of the leaves from the sheath out to the tip of the leaf. The writer observed this species on *Typha latifolia* at Ithaca in 1915, 1916, and 1918.

Aphis avenae Fab.[8]

The author found *Aphis avenae* Fab., the oat aphis, in large numbers, feeding on cat-tail, during the spring and summer of 1917, at Lawrence,

[7] Determined by Dr. Edith M. Patch.
[8] Determined by J. J. Davis.

Kansas. Frequently the young aphids were found behind the sheaths of the leaves, in the gelatinous material below the surface of the water in which the plants were growing.

Rhopalosiphum dianthi Schrank

Rhopalosiphum dianthi Schrank was reported on cat-tail by Sanborn (1906).

Rhopalosiphum persicae Sulz.

Rhopalosiphum persicae Sul. was reported on *Typha latifolia* and on *T. angustifolia* by Wilson and Vickery (1918).

Aphis gossypii Glov.

Aphis gossypii Glov. is found in small numbers on *Typha latifolia* during the spring and fall, according to Davidson (1917:65).

Macrosiphum granarium Kirby

Macrosiphum granarium Kirby, the grain aphis, is found in great numbers on Typha during the summer and fall, according to Davidson (1917:65).

Hyalopterus arundinis Fab.

Hyalopterus arundinis Fab., according to Davidson (1917:65), is found from April to June. The infestation on cat-tail is never large. There are four to ten generations. Aphids settle mainly on both sides of the blades, locating in colonies, usually not far from the tips.

HYMENOPTERA[9]

Five species of parasitic Hymenoptera were reared on insects which were found on cat-tails.

Aleiodes intermedius Cress

Aleiodes intermedius Cress was reared on larvae of *Arsilonche albovenosa*. On August 12, 1916, six specimens emerged from one larva.

[9] Determined by C. F. W. Muesebeck.

Apantales cinctiformis Vier.

Apantales cinctiformis Vier. was reared on larvae of *Nonagria oblonga*. A number of specimens emerged on August 8, 1916.

Elachertinae sp.

Five specimens of *Elachertinae* sp. were reared from a larva of *Lymnaecia phragmitella*. These emerged on June 15, 1916.

Pimpla indagatrix Walsh

On June 8, 1916, several specimens of *Pimpla indagatrix* Walsh emerged from the heads of cat-tails which had been kept in a covered jar in the laboratory.

Pimpla inquisitoriella D. T.

Several specimens of *Pimpla inquisitoriella* D. T. were reared from pupae of *Arsilonche albovenosa*.

DIPTERA[10]

The following flies were reared from cat-tail.

Platychirus quadratus Say

Platychirus quadratus Say was reared from the heads of cat-tail. The larvae were noticed in early spring in the overwintering cat-tail heads. Many adults emerged between May 21 and June 10.

Macrosargus clavis Will.

The larvae of *Macrosargus clavis* Will. live in the burrows made by the larvae of *Arzama obliqua* Walk. or of *Nonagria oblonga* Grote. They winter over in the larval stage, and the adults emerge in May and in early June.

Chaetopsis aeneae Wied.

The larvae of *Chaetopsis aeneae* Wied. also are found in the burrows of *Arzama obliqua* Walk. and of *Nonagria oblonga* Grote. Adults emerged on August 8.

[10] The first three species were determined by Dr. O. A. Johannsen, the last one by Dr. J. D. Tothill.

Sturmia nigrita Town.

Sturmia nigrita Town. is a parasite which was found living in the larva of *Arzama obliqua* Walk. In each of the two instances observed, there was only one parasitic larva present in each of the larvae of *Arzama obliqua*. Both dipterous larvae emerged from their host on March 25, 1918, through an opening which was made on the ventral side of the first thoracic segment. They pupated on the following day, and one adult emerged on April 9 and the other on April 10.

RÉSUMÉ

From an ecological point of view, the insect inhabitants of Typha may best be considered with respect to the part of the plant they affect. Accordingly they are thus classified in the following pages.

INSECT INHABITANTS OF THE HEAD OF TYPHA

The insects inhabiting the head of Typha include, among the Lepidoptera, *Lymnaecia phragmitella* Staint., *Dicymolomia julianalis* Walk., *Archips obsoletana* Walk.; and among the Hemiptera, *Ischnorrhynchus resedae* Panz.

The work of *L. phragmitella* and *D. julianalis* is very similar. Each has one generation a year. Their early larval habits are almost identical. They feed first on the tender styles of the pistillate flowers of the cat-tail plant, leaving the stigmas to form a covering over themselves. Later, they advance deeper into the head and feed on the seeds and other parts of the fruiting spike. Both overwinter in the half-grown larval stage. In the spring before pupation, however, their habits become somewhat different. Many of the larvae of *D. julianalis* bore into the rachis of the head, where they transform. The majority of the larvae of *L. phragmitella*, on the contrary, remain in the pappus of the cat-tail, where they pupate in closely woven cocoons. A few of the *L. phragmitella* larvae migrate down to the stalk of the plant, where they bore into the stems and transform. The adults of both species emerge at about the same time.

L. phragmitella is a species of world-wide distribution, while *D. julianalis* is generally restricted to the Southern States, though it is found as far north as New York. Of *L. phragmitella* the writer has found as many as 76 pupae in a single head, while of *D. julianalis* he has never observed more than six or eight individuals in one head.

Both of these insects are well adapted to live in the heads of cat-tail. Both spin an abundance of silk whereby they tie the pappus together and keep the head from being torn and the seeds from being scattered. This process of tying the pappus together assures the larvae of retaining their food supply and also furnishes them a protected and sheltered place for passing the winter. *D. julianalis*, however, being a less hardy southern form, was unable to stand the severe temperature during the winter of 1917–18, and all the larvae found in the Typha heads that spring were dead.

Archips obsoletana should probably be classified as an incidental feeder on cat-tail. It is a typical leaf-roller, occurring chiefly on strawberry plants. However, once the larvae locate on the head of the cat-tail, they spend the entire larval period there and transform to the pupal stage on the plant. Since there are three generations a year, it is very probable that never more than one generation is passed on cat-tail; for these insects feed only on the tender styles of the pistillate flowers, and as these soon dry up, the later generations would not be able to find the tender food they relish. When living on the strawberry plant, these larvae roll themselves up in a leaf for protection. On the head of cat-tails they protect themselves by tying the stigmas together underneath with a lining of silk, thus forming a cover under which they live while feeding on the styles of the flowers. When placed in a cage with cat-tail leaves, the larvae prepare a covering for themselves by tying two leaves together and crawling between them. At the time of pupation they tie a leaf to the head of the plant and thus obtain the protection necessary during their transformation.

In the spring, the females of *Ischnorrhynchus resedae* deposit their eggs in the old, downy heads of the cat-tail. The eggs closely resemble the seeds of cat-tail and thus are well protected from enemies. Immediately after hatching, the nymphs begin to feed on the seeds of the plant. They thrust their beaks into the dry seeds and apparently obtain their nourishment by injecting saliva into the seeds, which dissolves the solid material there so that they can suck it up into the body. The entire nymphal stage is spent in feeding on the dry seeds, a very remarkable and interesting adaptation. Due to the work of *L. phragmitella* and *D. julianalis*, the seeds of many of the old heads are kept from being scattered by the winter storms, and *Ischnorrhynchus resedae* simply takes advantage of these

conditions. It inserts its eggs into the pappus, where they are hidden from all enemies and where the nymphs find an abundance of food at hand which is not contested by any close relatives and which, indeed, is used by few other insects.

INSECT INHABITANTS OF THE LEAF OF TYPHA

The inhabitants of the leaf comprise two classes, the surface feeders and the leaf miners. The surface feeders include, among the Lepidoptera, *Arsilonche albovenosa*, and among the Hemiptera, the Aphidae enumerated on page 501. The most common of the surface feeders is the noctuid caterpillar, *A. albovenosa*. It is a general feeder but is very commonly found on cat-tail. The eggs are placed on the upper part of the leaf, and the larvae, as soon as hatched, feed on the leaf. A leaf thus infested has the appearance of having been skeletonized. After they grow larger, the larvae begin feeding on the edge of the leaf, where they eat out large sections.

The species of aphids mentioned on pages 500–501 may be classed as feeders on the leaf, although they occasionally feed lower down on the stem and sheaths of the plant.

The leaf miners include *Arzama obliqua* Walk. and *Nonagria oblonga* Grote. These two noctuid larvae do not restrict themselves entirely to leaf mining but they begin their larval life as leaf miners, later becoming true stem borers. Although the two species are related, their habits differ greatly. *A. obliqua* overwinters as a larva in its burrow in the cat-tail plant, whereas *N. oblonga* apparently passes the winter in the egg stage. The eggs of *A. obliqua* are laid in the spring, while those of *N. oblonga* are apparently laid in the fall. The young larvae of *A. obliqua* burrow gregariously, but the larvae of *N. oblonga* are solitary miners. The nature of their mines, too, is very different. *A. obliqua* advances down the channels of the leaf, leaving the longitudinal partitions of the leaf intact and only destroying the cross partitions, while *N. oblonga* produces a sort of blotch mine by zigzagging back and forth in the leaf and destroying both the longitudinal and the transverse partitions. Both species feed mainly on the chlorophyll of the leaf. When ready for the first molt, *A. obliqua* sheds its skin at once, right in the mine, near the healthy, undisturbed, succulent tissue of the leaf; but *N. oblonga*, when ready for its first molt, first severs the connecting tissue of the leaf in order to

produce a drier situation in which to cast off its coat. This variation indicates that *A. obliqua* is better adapted than *N. oblonga* to live in moist or wet situations. A comparison of the tracheal systems of the two larvae shows this yet more clearly. *A. obliqua* has the spiracles of the eighth abdominal segment located on the dorsal surface and they are more than twice the size of the other spiracles of the body. Directly attached to these spiracles are the two longitudinal tracheal trunks of the body. Segment 9 of the abdomen is flattened dorsally so as to be only half as thick dorso-ventrally as the other abdominal segments, thus making room for the large spiracles on the eighth segment. This allows the body of the larva to be almost entirely submerged in the water, for as long as these spiracles remain above the surface it suffers no harm. The tracheal system of *N. oblonga* has not undergone any such modifications, however. The spiracles on its eighth abdominal segment are located in the natural position and are the same size as the other abdominal spiracles. Consequently the larva is likely to suffer harm if much water gathers in the burrow, as often occurs in wet situations. The larvae of *A. obliqua* remain in the leaf of Typha only through the first instar, while the larvae of *N. oblonga* often remain in the leaf through the second and even the third instar. The nature of their mining habits may have much to do with the difference. *A. obliqua* does not destroy the longitudinal partitions of the cat-tail leaf, and consequently must get out after its first molt on account of its increased size in the second stage. *N. oblonga*, however, cuts through the partitions in any direction and so is able to remain in the leaf for a longer period. After leaving the leaf, both larvae become solitary borers in the stalks of cat-tail.

INSECT INHABITANTS OF THE STALK OF TYPHA

The insects which work in the stalks of the cat-tail include two species of the Lepidoptera, *Arzama obliqua* Walk. and *Nonagria oblonga* Grote, and the Coleoptera, *Calendra pertinax* Oliv. and *Notaris puncticollis* Lec.

After the larvae of *A. obliqua* and *N. oblonga* leave the mines of the leaf, they become stem borers. Their methods of entering the stem are very similar. Both are frequently found feeding for a time behind the sheaths of the outer leaves of the plant. From the sheath they either bore directly into the stem or enter from between the leaves of the leaf bundle. Both work their way to the center of the plant and locate at

the point where the tender new tissue is forming. The effect of their work on the plant is very similar: the central leaves of the leaf bundle die and the plant fails to produce a fruiting stalk.

C. pertinax, the weevil, begins its larval life as a stem borer, later becoming a borer in the rhizome of the plant. The eggs of *C. pertinax* are inserted into the sheaths of the plant, near the ground. The newly hatched larvae bore to the center of the stalk and hollow it out just above the crown, thus arresting the further growth of the plant. After feeding on the tender tissue at the center of the stem for some time, the larvae enter the rhizome and there feed on the more substantial starchy food. When full-grown, the larvae return to the stalk and there form a pupal chamber in which the transformation takes place. There is only one generation. The larvae are ordinarily solitary borers, although as many as seven larvae have been found in one plant.

INSECT INHABITANTS OF THE RHIZOME OF TYPHA

The inhabitants of the rhizome are the Coleoptera, *Calendra pertinax* Oliv. and probably *Notaris puncticollis* Lec. The larvae of *C. pertinax* feed during the major part of their larval period on the starchy core in the rhizome of the plant. By first tunneling out the center of the stalk at the crown of the plant, they prevent the formation of new leaves, and in this way the larvae cause the starch to remain in the rhizome for their nutriment which would otherwise be used up in the growth of the plant. The leaves already formed are left undistrubed to manufacture and send down more starch to the rhizome. Very likely the habits of *N. puncticollis* are similar to those of *C. pertinax*.

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PLATE XXXIX

TYPHA LATIFOLIA

1, Sterile seed, showing large size of pericarp. 2, Fertile seed. (The pericarp fits closely over the kernel.) 3, Seed, or kernel, removed from pericarp. 4, Embryo protruding through pericarp. 5, Same as 4, with pericarp removed. 6, Growing embryo as it appears when removed from seed. 7, Embryo pushing open cap of seed. 8, Beginning of formation of root. (The arrow indicates the developing leaf.) 9, Further development of young plant. (The leaf has protruded and root hairs have developed on the root.) 10, Young plant with three leaves and three roots, showing disintegration of tip of first leaf, whereby it frees itself from the seed

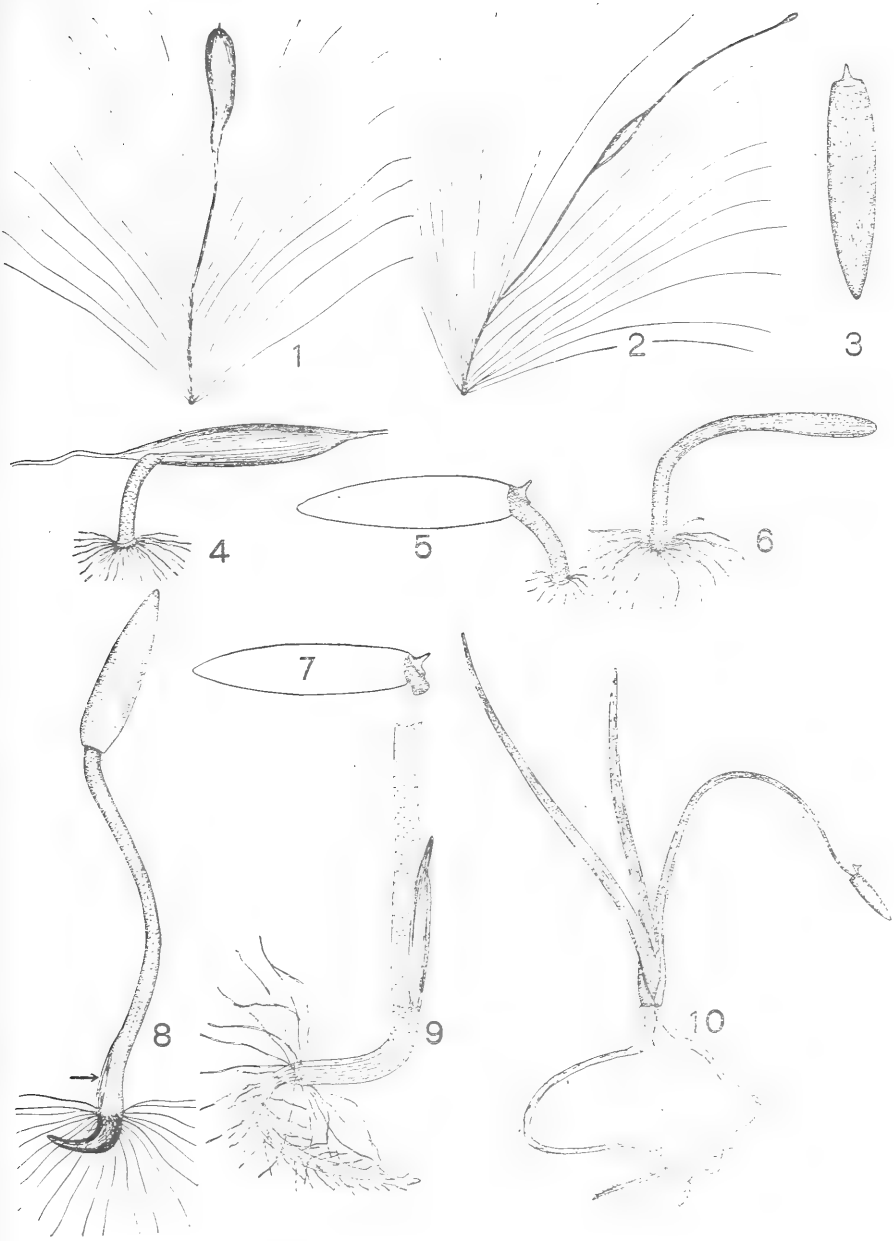
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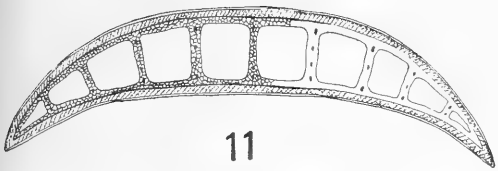
PLATE XL

TYPHA LATIFOLIA AND CALENDRA PERTINAX

Typha latifolia: 11, Cross section of leaf. 12, Cross section of a small part of leaf, showing more detail. 13, Cells of rhizome filled with starch grains. (Dormant season.) 14, Part of 12 enlarged to show structure of epidermis, chlorophyll, supporting tissue, and vascular bundles. 15, Cells of rhizome partly filled with starch grains. (Growing season.) 18, New offsets

Calendra pertinax: 16, Egg. 17, Egg inserted in sheath of cat-tail. 19, Rhizome of cat-tail cut open to show larval work. 20, Newly hatched larva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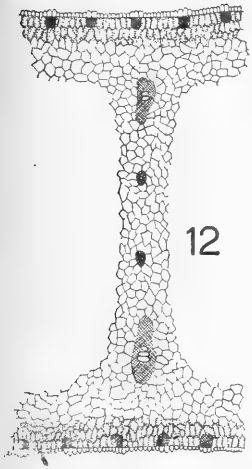
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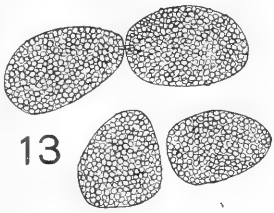
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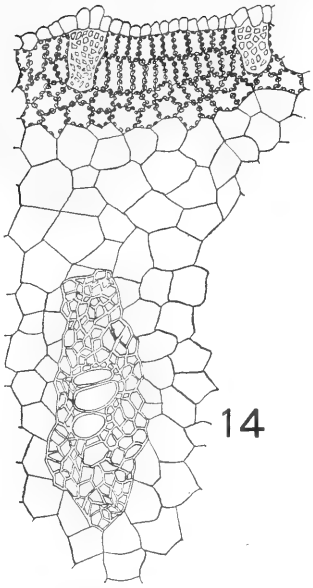
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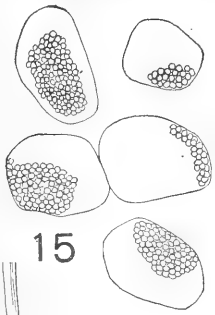
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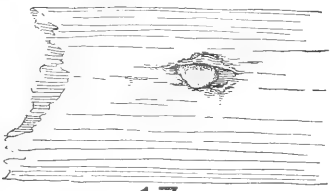
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PLATE XLI

ARZAMA OBLIQUA

21, Egg. 22, Full-grown larva. 23, Pupa. 24, Egg mass on cat-tail leaf. (The larvae have emerged and mined along the middle part of the leaf, thus causing the center to die.) 25, Cat-tail leaf with egg mass, showing mine and exit holes of larvae. 26, Adult female. 27 and 28, Full-grown overwintering larvae in stalks of cat-tail. 29, Newly hatched larva. 30, Dorsal view of caudal segments of larva, showing position of spiracles on eighth abdominal segment. 31, Tracheal system of full-grown larva. (Only the first one of the five branched tracheal tubes is shown in its entire length)

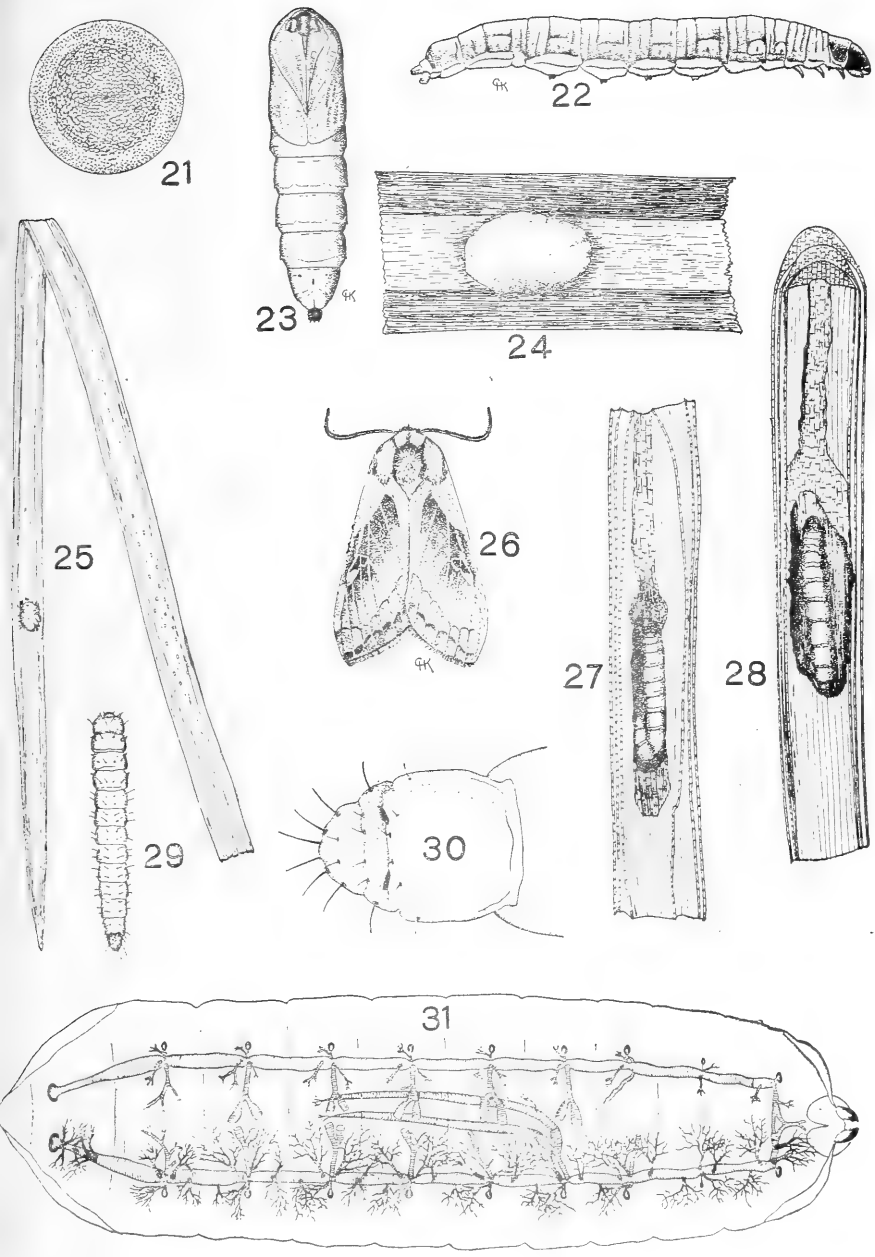
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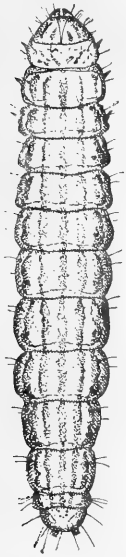
PLATE XLII

LYMNAECIA PHRAGMITELLA AND NONAGRIA OBLONGA

Lymnaecia phragmitella: 32, Full-grown larva. 34, Pupa. 35, Stalk of cat-tail with leaf turned aside to show where larvae have tunneled in, preparatory to pupation

Nonagria oblonga: 33, Pupa. 36, Cat-tail plant showing work of larvae. (The first-stage larvae have cut the leaf. A mine appears also in the outer sheath.) 37, Cat-tail leaf showing early larval work. (The arrow points to the cast skin of the first molt in the transverse mine)



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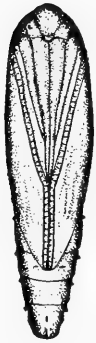

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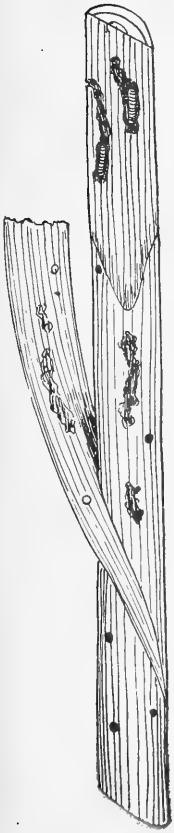

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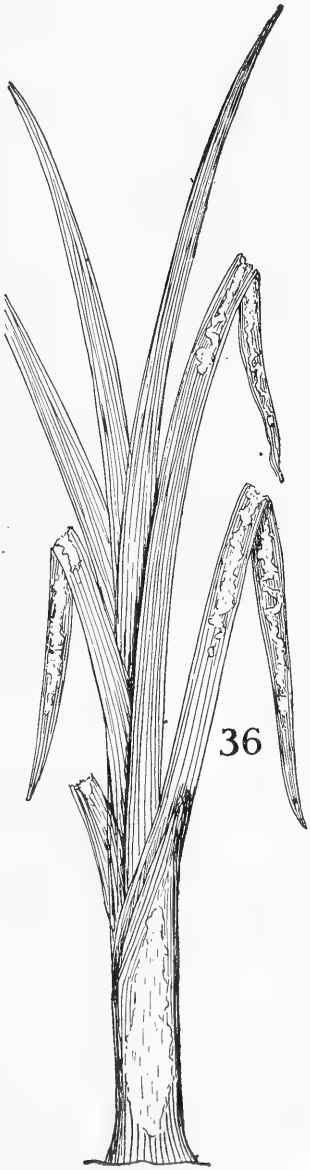

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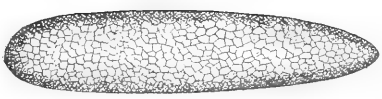
PLATE XLIII

DICYMOLOMIA JULIANALIS

38, Egg. 39, Reticulations on surface of egg. 40, Newly hatched larva. 41, Full-grown larva. 42, Axis of cat-tail head cut open to show larval work. 43, Axis of cat-tail head, showing opening of larval tunnels. 44, Pupa. 45, Cross section of head of cat-tail, showing location of eggs (indicated by *a*). 46, Empty egg shell after emergence of larva



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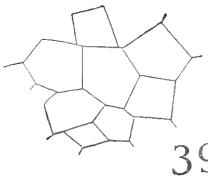

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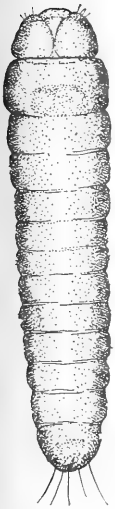

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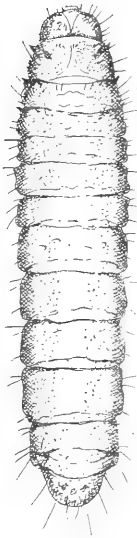

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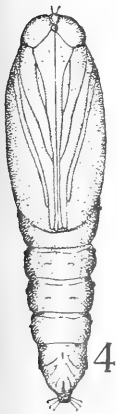

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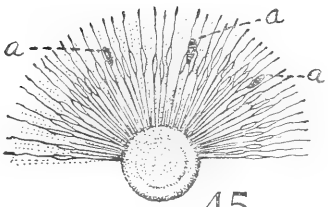

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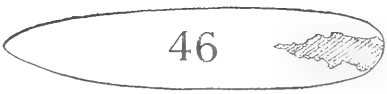

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PLATE XLIV

ISCHNORRHYNCHUS RESEDAE

47, Egg. 48, First-stage nymph. 49, Fourth-stage nymph. 50, Third-stage nymph. 51, Second-stage nymph. 52, Adult female. 53, Enlarged drawing of beak of nymph inserted in seed of cat-tail. 54, First-stage nymph. 55, Fifth-stage nymph feeding on seed of cat-tail

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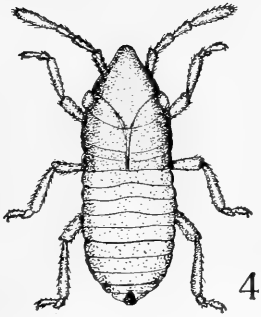

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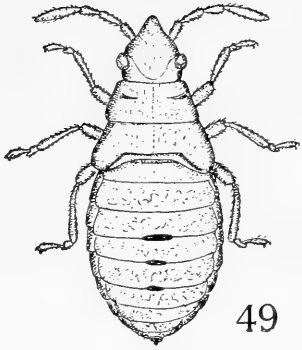

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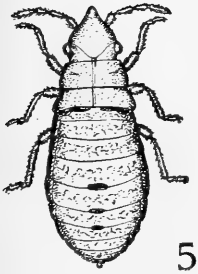

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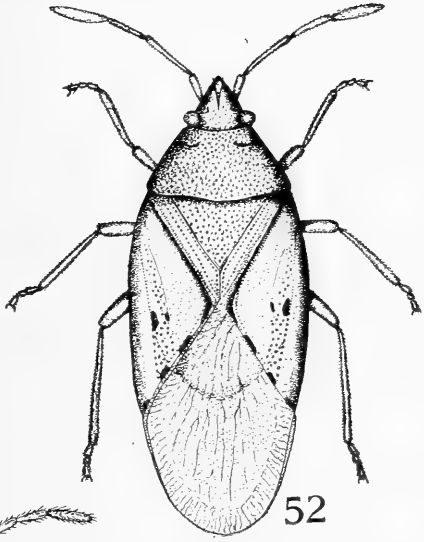

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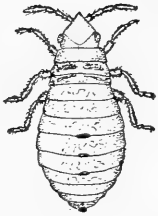

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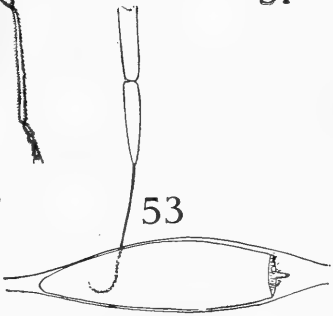

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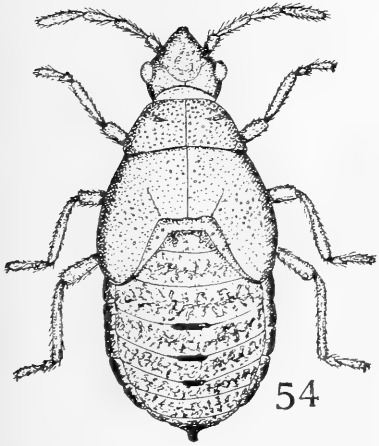

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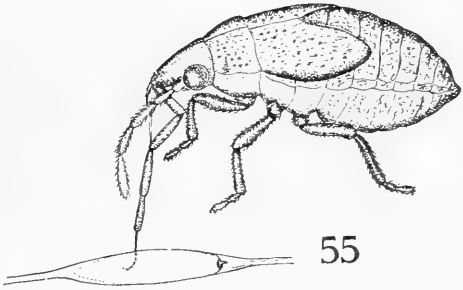

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PLATE XLV

TYPHA LATIFOLIA

56, Two plants connected by underground rhizome, showing also new offsets at bases of old plants. 57, Two pieces of rhizome with outer covering removed to show the relative size of the central starchy core. 58, Leaf with part of the upper epidermis removed to show the structure. 59, Cat-tail heads as they appear in late fall. (The one on the left is infested with the larvae of *Lymnaecia phragmitella;* the one on the right is uninfested.) 60, Cross section of a rhizome

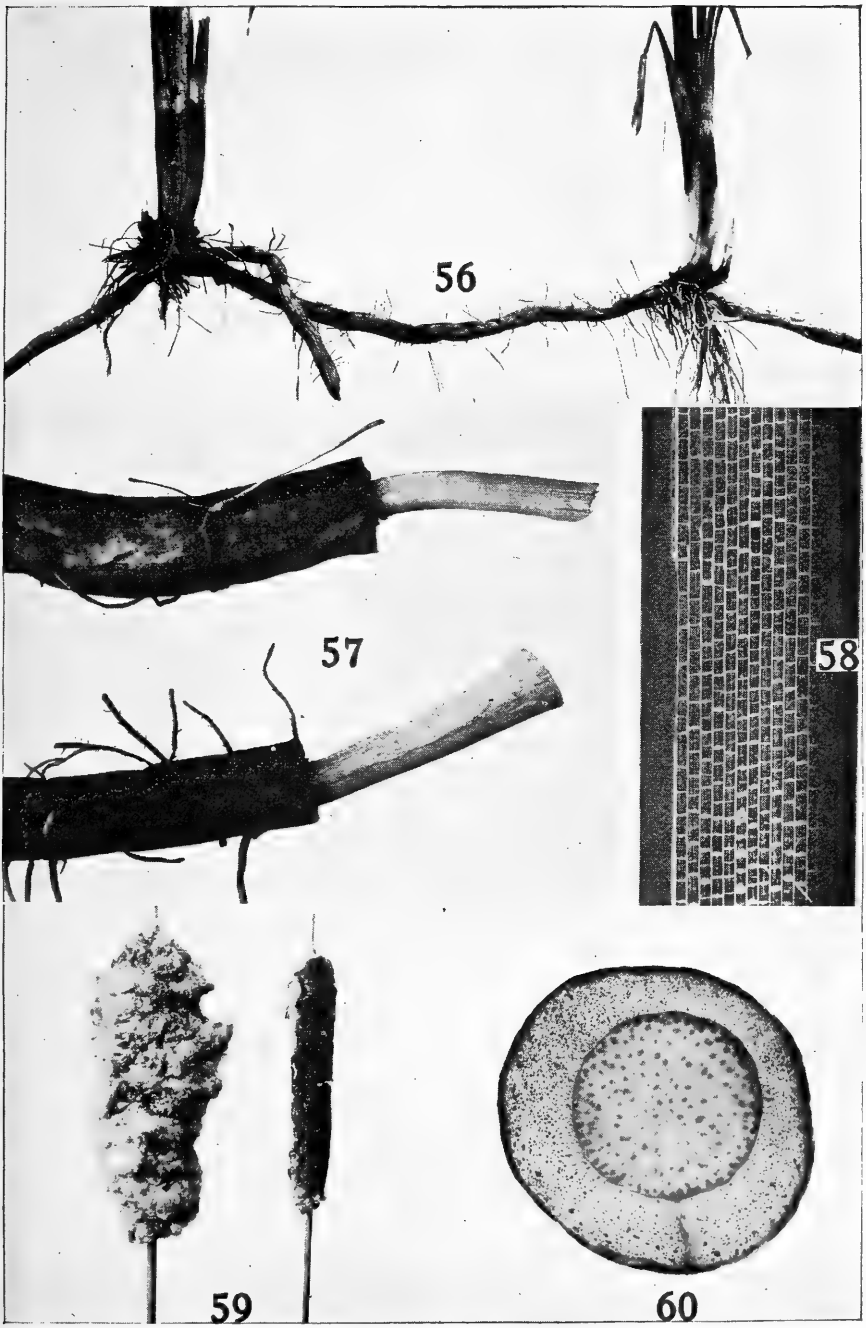
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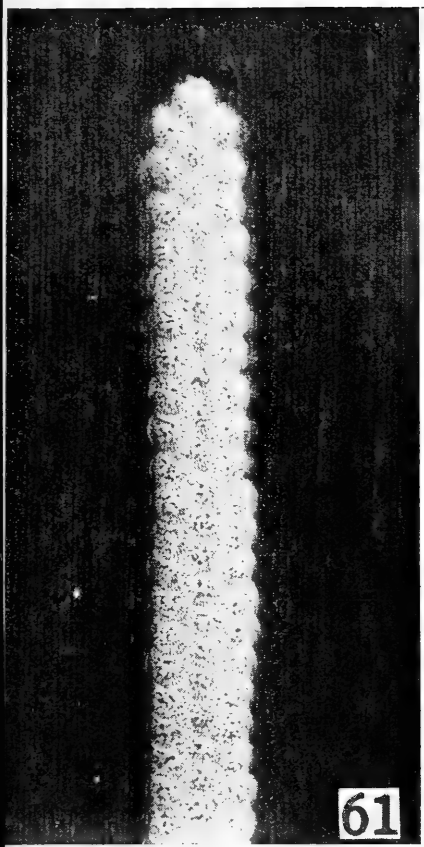
PLATE XLVI

ARSILONCHE ALBOVENOSA AND ARZAMA OBLIQUA

Arsilonche albovenosa: 61, Eggs. 62, Larva feeding on cat-tail leaf. 63, Pupa. 64, Adult
Arzama obliqua: 65, Egg mass. 66, Full-grown larva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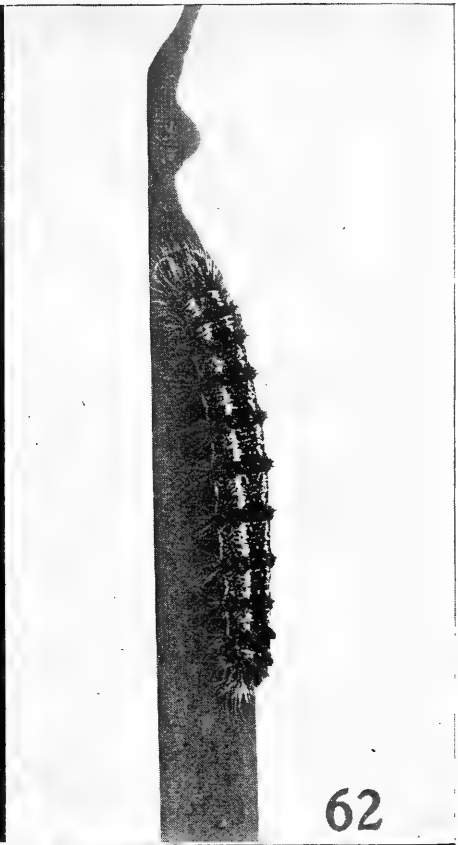
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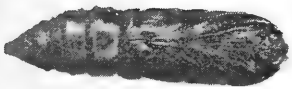
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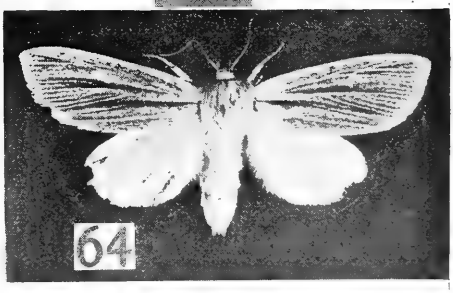
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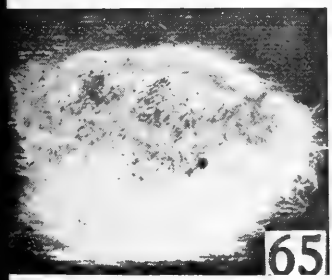
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PLATE XLVII

NONAGRIA OBLONGA AND ARCHIPS OBSOLETANA

Nonagria oblonga: 67, Full-grown larva. 68, Adult. 70, Larva in tunnel in stalk of cat-tail. 71, Pupa

Archips obsoletana: 69, Young cat-tail head showing larval work. (The covering is pulled aside, revealing the head of the larva underneath.) 72, Young cat-tail head showing larval work. (The stigmas of the pistillate flowers are tied together to form a covering for the larva.) 73, Appearance of cat-tail head after wind has torn off covering made by larvae. 74, Pupa. 75, Adult. 76, Larva

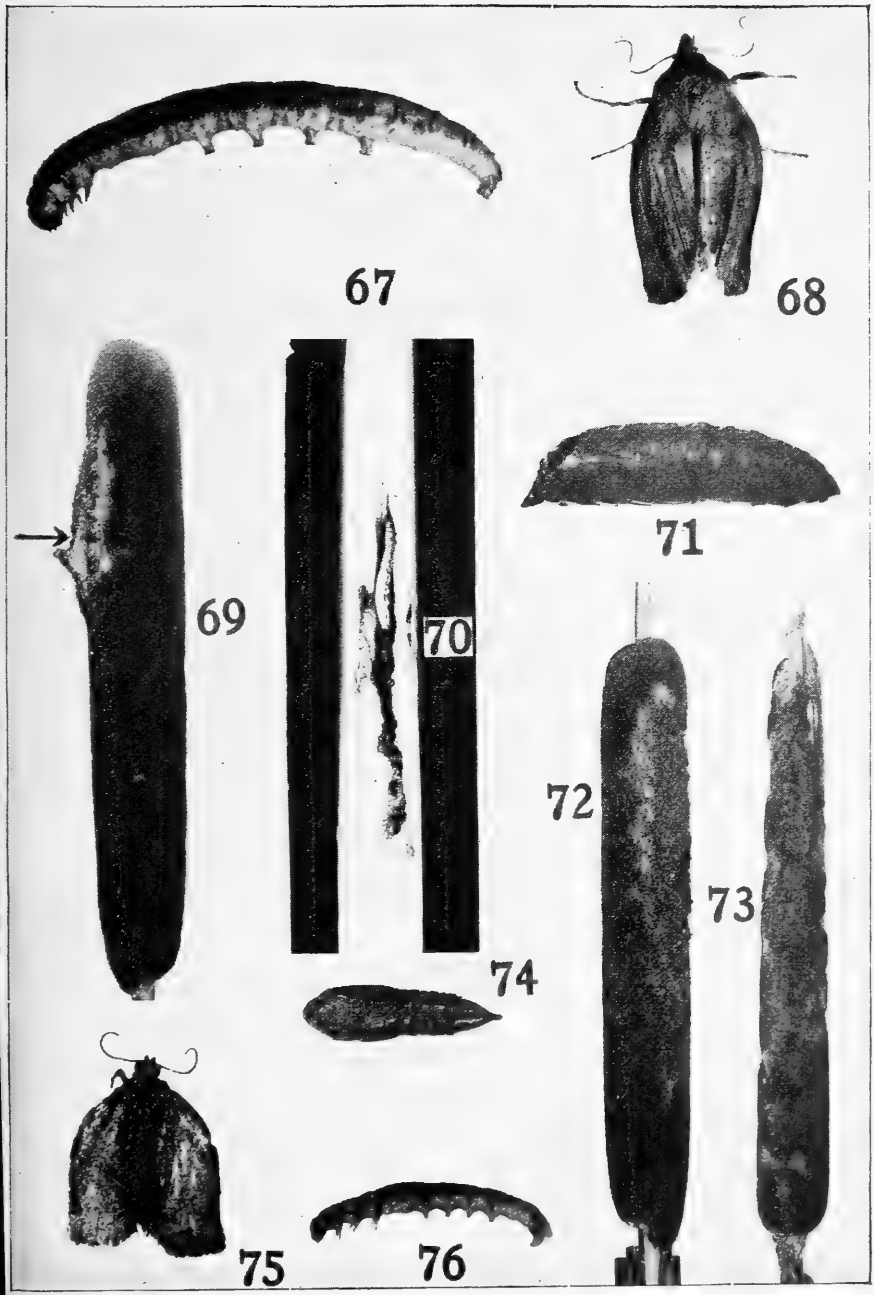
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PLATE XLVIII

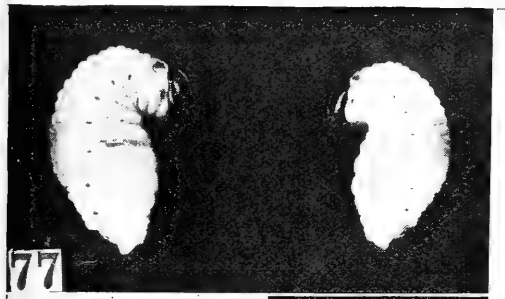
CALENDRA PERTINAX, DICYMOLOMIA JULIANALIS, LYMNAECIA PHRAGMITELLA, AND NOTARIS PUNCTICOLLIS

Calendra pertinax: 77, Larvae. 78, Adult. 79, Pupa. 80, Pupa in burrow in stalk of cat-tail

Dicymolomia julianalis: 81, Adult

Lymnaecia phragmitella: 82, Cocoons removed from cat-tail head. (One is cut open to show pupa inside)

Notaris puncticollis: 83, Adult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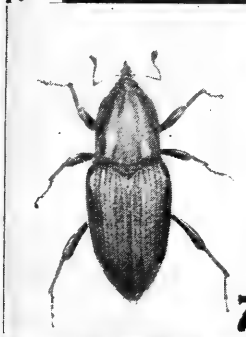
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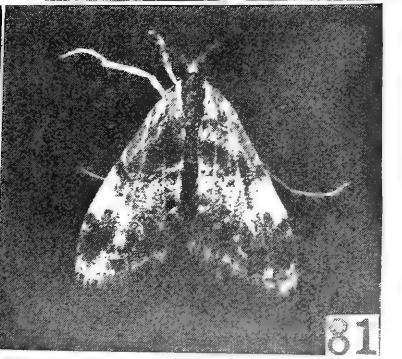
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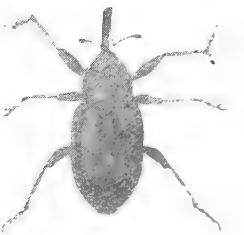
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PLATE XLIX

TYPHA LATIFOLIA

84, A cat-tail patch in July, showing the large number of fluffy heads which are infested with the larvae of *Lymnaecia phragmitella*. 85, Laboratory cat-tail head on which adults of *L. phragmitella* are resting. 86, Nearly mature head of cat-tail, showing evidence of work of young larvae of *L. phragmitella* and *Dicymolomia julianalis*

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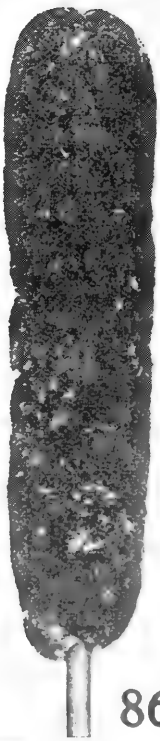

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THE BIOLOGY OF EPHYDRA SUBOPACA LOEW

CHIH PING

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CONTENTS

THE BIOLOGY OF EPHYDRA SUBOPACA LOEW

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CHIH PING

The observations and experiments herein described were begun in the summer of 1916 and covered a period of two years. The main purpose of the study was to investigate the habits, activities, and relations to environment of *Ephydra subopaca* throughout all the stages in its life history, and to solve the problem of its unique habits and adaptations. During the period, daily field data were taken at the salt pools beside the east bank of Cayuga Lake, and various other salt-water areas in the vicinity of Ithaca, New York, were occasionally visited.

HISTORY OF THE SPECIES

The adult of this species was first described by Loew (1864) from Connecticut. Following this, Packard (1868) described both the puparium and the adult as *Ephydra halophila* (a preoccupied name), from brine pools in Illinois. The occurrence of this species at Charlotte Harbor, Florida, was recorded by Johnson (1895), and at several localities in New Jersey by Smith (1890). Johnson (1904) also records this species at Atlantic City and Seaside Park, New Jersey. All the works mentioned above are mere descriptions or records of occurrence, but none has anything bearing on habits, development, or life history. The most recent and detailed work on the biology of *Ephydra subopaca* is by Aldrich, in whose article on some western species (1912 a) are discussed the habits, food, and some interesting features of both the adult and the immature stages. However, the egg was not described, oviposition and mating had not been observed, and the life history was hitherto incomplete. Neither had ecological phenomena been investigated in detail.

DISTRIBUTION AND RANGE IN ITHACA AND VICINITY

Only two species of Ephydra, as far as records show, are found in New York State. The species *Ephydra subopaca* is found in Ithaca and in

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neighboring localities wherever salt pools occur. The larvae and pupae live in water of various densities and in a variety of other physical conditions, but a certain percentage of salt must be present in the water. The species can live in fresh water only for a very brief period. The species was found living at two places in Ithaca, the first being an old salt plant, near the Inlet, where there were two permanent pools, in which the water was brownish in color and salty in taste. All stages of the species were collected here in the summer of 1916, but unfortunately, in the year following, one pool was filled with dirt, while the other one became entirely fresh, and no more of this species could be found there.

The second place where this species was and can yet be found, is at the east bank of Cayuga Lake, at the Remington Salt Works, where the salt wells are the sources of the overflow of brine water from an intensive area. At this place the water is strong in salt, and the pools, ditches, and overflowed areas abound in *Ephydra subopaca* in all stages of development. Throughout the two summers and a part of the winter of 1916–17, most of the field observations were made at this latter place and practically all the ecological phenomena discussed herein are related to this locality.

At Ludlowville, on the east shore of Cayuga Lake, a fairly wide area is flooded at certain seasons by the brine water from salt wells. This condition is by no means permanent, and the salt water is frequently dried up in midsummer. However, in the summer of 1917 this place was visited at intervals for making observations and for collecting. Next to the permanent pools at Ithaca, the best place, where enormous numbers of this species are found and where the permanent pools, ditches, and wide, overflowed areas afford excellent opportunities for field work, is at Solvay, Syracuse.

Owing to convenience of location, most of the ecological observations were made at the salt pools at Ithaca. There are eight pools, six of which are located in series, about one and a half meters apart, situated from north to south along the east side of the lake. The six pools are designated as A, B, C, D, E, and F. The other two, I and II, are situated farther away from the lake shore, toward the east, and along the roadside. In addition to the eight pools, overflowed areas, large and small, are scattered here and there between the pools, covering an estimated area of forty square meters.

PHYSICAL FEATURES OF SALT POOLS

Soil

Although these pools are scarcely over a year old, due to the destruction and reconstruction of the salt works within two years, the physical features in them are perfectly natural. Pools A to F are located close to one side of a delta deposit of Hamilton shales on the east shore of Cayuga Lake. The soil at the east side of the pools is largely made up of such deposit and is elevated about one meter higher than the soil at the other side, which is on the ground level. The soil of the higher side has shales mixed with clay, while that of the lower side, which composes three-fourths of the circumference and slopes down to the bottom, is entirely free from shales and is a homogeneous, purely clay soil.

The condition in pools I and II, and in the overflowed areas, is entirely different. The overflowed areas are composed of sandy loam with some organic materials, such as grass stems, and with small fragments of boards and animal excrement sparingly scattered over.

Pools I and II, in which the water is much deeper, possess some different features as far as soil is concerned. They are situated quite away from the delta deposit, and no shales have been found in them. One side of these two pools is adjacent to a path built up with a mixture of cinders and sandy loam and their bottoms are on the same ground level with the overflowed areas. Glancing into the pools through the transparent and comparatively fresh brine water, the homogeneous grayish black color of the soil affirms that the entire bottom and the slopes below the water surface consist of nothing but sandy loam mixed with coarse cinders.

Water

The pools, in contrast to the overflowed areas, are permanent. The general condition of the water varies according to rainfall, sunshine, salinity, and biological content, and sometimes to artificial causes also. The average diameter of these pools measures from 1.35 to 1.4 meters, and the depth from 0.35 to 0.4 meter; that of the overflowed areas, from 5 to 6 centimeters. The color of the water in pools A to F is generally brownish. When rainfalls are frequent, the brownish color fades away, changing to slightly grayish green about 3 or 4 centimeters below the surface. The water in the overflowed areas remains fairly clear owing to its shallowness

and temporary existence. Generally a thick layer of dark brown scum prevails here and there over the surface, but the clearness of the water underneath is not affected. Pools I and II were dug in the latter part of the summer of 1917; unlike the water in the older pools, the water in these has continued perfectly clear all the time, so the presence or absence of color is due to the difference in age of these pools. Pools A to F, because of their proximity to a much-used rail track, have been polluted to a certain extent by oily substances and animal feces. This is true also of some parts of the overflowed areas. Pools E and F were spoiled in the latter part of the season by being filled in with lumber fragments and a great quantity of waste salt. The general condition of the water in the different pools from August 17, 1917, to October 17, 1917, has been recorded as follows:

Pool	August 17	August 19	August 22	September 7	September 18	October 3	October 17
A	Greenish brown	Pale greenish	Greasy films	Greasy films	Greasy films, grayish	Greasy films, grayish	Greasy films, grayish
B	Green, brownish at surface	Pale greenish	Somewhat clear, thin greasy films	Clear, slightly pale greenish	Greasy films, greenish	Greasy films, greenish brown	Greasy films, grayish
C	Brownish, slightly dark	Pale greenish	Thin greasy films	Thick greasy film, brownish	Pale greenish brown	Pale greenish brown	Greasy films, grayish
D	Brownish, slightly dark	Brownish	Thin greasy films	Deep green	Greenish brown	Greenish brown	Brownish
E	Somewhat clear	Brownish	Spoiled				
F		Brownish	Spoiled				
I, II	Clear throughout the season						

The water in all these pools, as well as in the overflowed areas, remains stagnant all the time. When rain is in excess, water may flow into them from the near-by ditches or from some areas that are located on a higher level; but throughout the greater part of the season the stagnant condition is seldom disturbed. The quantity of water in these pools is decreased by evaporation during dry weather. The pools themselves, however, did not dry up during the seasons of observation. Being so limited in area and so sheltered in location, the surface of the pools is not likely to be disturbed by the wind.

Although situated close to one another, the density and salinity in the pools have noticeable fluctuations and increase from north toward south in their range; this is perhaps due to their gradual approach to the spot where the loading of salt takes place, which is near Pool F. The following shows the difference:

Pool	Density		Salinity (per cent)	
	August 10*	September 22†	August 16‡	August 16§
A	1.5	4	3.90	1.90
B	2.0	5	1.76	2.28
C	4.0	6	2.68	5.35
D	5.0	6	4.20	6.84
E	7.0	.....	5.58	9.70
F	7.0	.....	7.40	9.70
I	.....	9	.....	.....
II	.....	11	.....	.....

*Determined in the laboratory.
†Determined in the field.
‡Analyzed after one day in the laboratory.
§Analyzed after being kept for three days in the laboratory.

BIOLOGICAL CONTENTS OF SALT POOLS

As the pools are so limited in size and since none of them have been in existence for more than a year, it is only natural that no large plants have ever been found growing in them. Moreover, the salinity and density of the water account for the total absence of some larger animals that commonly inhabit fresh water pools. The only fauna and flora that are common here are plancton forms, the plants of which serve as food through-

out the season for *Ephydra subopaca* in both the larval and the adult stages when active. The plancton enriching pools A to E gives color to the salt water in very different degrees. Plancton is the only organic material from which the inhabiting fauna obtains its subsistence. In the summer season the changing colors and varying content of the water in these pools mark the increase and decrease in abundance of the microscopic forms of one kind or another. During frequent surveys of pools A to F made in the middle and later part of the summer, it was found that the plant life therein included large numbers of Chlamydomonae, Navicula, and bacteria, and the animals, numerous Actinophrys and Monas, a few Astasia and amoebas, and a very few Halophrys and Ciliata.

The green color of the water in the pools is due to the presence of an abundance of green algae, chiefly Chlamydomonae, and the brownish tinge is caused by the increase of diatoms, namely, some species of Navicula and its allies. These are the two most prominent forms of plant life in the pools.

As before stated, pools I and II were formed later than the others, and their water remains clear all the time; accordingly in them the biological content is more meager, consisting of a small number of Navicula, Chlamydomonae, and one or two ciliated protozoa. In late summer, however, a noticeable change takes place. At the bottom of these pools a thin layer of brownish organic matter is formed, largely made up of Navicula with comparatively few Chlamydomonae. This deposit does not affect the transparency of the fresh brine water.

Owing to the wide area and exposed surfaces which are easily reached by sunshine, thick, foamy, brown scums are found here and there on the surface of the shallow water in the overflowed areas. These scums afford the larvae, especially during early stages, shelter and shade when the sun's rays at noontime are too strong; they act as a moisture retainer when the areas are rapidly drying up; and finally, for the larva as well as the adult, they constitute a main source of food supply. These floating scum masses embody the entire fauna and flora in the shallow water.

In comparing the two sets of pools—A to F, and I and II and the overflowed areas— it was found that in the former group green algae predominated, with the protozoa more numerous, while in the latter group the brown algae were in greater abundance.

LIFE HISTORY

THE LARVA

Morphology

Various methods were tried for studying the anatomy of the larva. The following methods yielded the most satisfactory results.

For the muscular system, it was found that specimens were best fixed in slightly warm Bouin's or Gilson's solution. Both the cutaneous and the cephalopharyngeal musculatures appeared opaque white, and were thus to be distinguished from other structures. For the nervous, alimentary, tracheal, and vascular systems and the imaginal disks, 10-per-cent formalin seemed best. The fine branches of the nerves and tracheae were preserved intact and were recognized and distinguished from one another under a binocular microscope with the aid of bright sunlight or the artificial light of a nitrogen-filled lamp. The imaginal disks were best studied by staining with diluted methylene blue (5 drops to 5 cubic centimeters of water); this distinguished them from the nervous ganglions, which do not take the stain to the same degree. The dorsal vessel, the ring, and the entire alimentary system were preserved in perfect condition in this weak fluid. In checking up the gross dissections, serial sections were cut from 5 to 10μ with a microtome. Here again Bouin's and Gilson's solutions were the fixers used. The following was the procedure: Certain parts not to be studied were snipped off in order that the fixer might penetrate quickly. The specimen was killed in hot solution and fixed for from 12 to 24 hours, washed in 85-per-cent alcohol which was changed three or four times a day, and stained *in toto* in borax carmine for from 24 to 48 hours. The specimen was then de-stained in 70-per-cent acidulated alcohol for from 12 to 24 hours, in 85-per-cent alcohol for 24 hours, in 95-per-cent alcohol for 24 hours, in absolute alcohol and cedar oil for 24 hours, in cedar oil for 24 hours, in 56° paraffin for 24 hours; section from 5 to 10μ; xylene 5 minutes; in 95-per-cent alcohol 5 minutes; in carbol-xylene for 5 minutes. Lastly, the specimen was mounted in balsam.

External structures

General features.— The body of the larva consists of twelve segments. The first, or head, segment is often retracted and not visible from

above. The second, or first thoracic, segment is partly retracted and a pair of sense papillae are visible both laterally and ventrally. Owing to the retraction of these two segments, there results an oval opening or invagination, bordered by the fold of the integument of the first thoracic segment, situated cephalo-ventrad at the anterior end of the larva. In the specimens fixed in Bouin's or Gilson's solutions, the wrinkles in the integument are flattened out, and the first two segments are stretched and distended, so that they can be easily examined; but the segments throughout the whole body are not very distinct externally.

The shape of the body is more or less cylindrical. The body tapers off gradually from the third segment toward the anterior end, while the diameter increases from the twelfth segment toward the posterior end; but for the most part the diameter of the abdominal segments is fairly uniform. The caudal process is circular in cross section and terminates with a more or less truncate end, where two cylindrical branches arise. Through these branches the main trunks of the tracheal system come to the exterior. The average length of the full-grown larva (Plate LIV, 2), including the caudal process with its branches, is 12 millimeters.

The integument.— In the young larva the integument is grayish in color, and is thin and more or less transparent, so that some of the internal organs can be seen through the skin. The body is more or less hairy. In the mature larva the hairs on the dorsum are more pronounced than those on other parts of the body. On the dorsum are seven somewhat V-shaped blotches, the hairs of which are modified into flat scales. The prothoracic segment is covered with short and blunt bristles.

In cross section the cuticular integument is composed of two layers. The outer layer is thin and slightly chitinous, bearing the chitinous hairs, while the inner layer is very thick and homogeneous in structure. Underneath the two layers is a thin layer of hypodermis. The writer has never been able to see the hexagonal cells of the hypodermis as mentioned by Trägårdh (1903). However, the large oval nuclei of these cells are very conspicuous.

The appendages.— The very short antennae, each consisting of two joints, are above the prominent oval lobes and are scarcely visible at all when the head is retracted. A pair of chitinous prothoracic stigmas, each consisting of four digits, are borne one on each side in the second segment. The stigmas are ordinarily visible, but sometimes, by the

retraction of the first two segments, they are entirely concealed within the fold of the integument. The thoracic segments are footless, while each abdominal segment bears a pair of prolegs. These prolegs are nipple-shaped, are fused at the basal third, and bear a number of claws on their blunt tips. These claws are arranged in three rows, usually with five in the first, four in the second, and four or five in the third. The number varies and the size of the claws decreases row by row. In addition, there is one more row of rather insignificant small claws. The last pair of prolegs are more prominent than any of the preceding ones, and the claws upon them are much larger. The claws here are opposed in position to those on the other prolegs. This enables the larva to grasp an object by means of these and the two preceding pairs, when pupation is impending.

Behind the anal opening is a pair of more or less rounded pads which are considered as parts of the prolegs, and a number of small claws are borne on them. The caudal process is a cylindrical sheath, into which its two branches can be withdrawn. It is longer than any segment in the body of the larva, being about three or four times as long as the twelfth segment. At the end of each branch of the process is a chitinous cap with one large round pit situated at the center and four small openings on a chitinous knob surrounding this pit. At the inner border of each of these openings is attached a fan-shaped thin membrane, which can be seen best when the larva sticks its caudal tips to the surface of the water for respiration (Plate LIV, 7).

Internal structures

The tracheal system.— The tracheal system consists mainly of two pairs of longitudinal trunks, one dorsal and one ventral. The dorsal trunks are large and are the true trunks, while the ventral are more delicate and are made up merely by the connection of the outer branches of the dorsal pair (Plate LIV, 8). The dorsal pair begins in the second segment where the prothoracic stigmas open out through the body wall, and extends posteriorly to the caudal tips, which bear the spiracles. Connecting these two main trunks in the fourth segment is a commissure, overlying the cephalopharyngeal skeleton. Trägårdh states that in *Ephydra riparia* this is the only commissure, but the writer has found in *Ephydra subopaca*, in the caudal region close behind the twelfth segment, a very short commissure concealed by the crossing of the two tracheal trunks.

In addition to the two just mentioned, another one is found in the ninth segment. This commissure, however, is not so large as the anterior one and it might easily be confused with some of the inner branches from the trunks.

As the larva is amphipneustic, each dorsal trunk has its anterior and its dorsal spiracles. The anterior spiracles are lacking in the young larva during the first instar. The anterior spiracular process consists of a hand-shaped body bearing four digits, although sometimes only three are present. Each digit has a small opening at the tip (Plate LIV, 6). The posterior spiracles are found in the larva shortly after hatching. At this time, the caudal process, however, is not well developed. At the caudal end there appear two oval disks (Plate LIV, 4), which become the tips of the future caudal branches. In the center of each disk are two metallic shining chitinous knobs with a small round pit closely mesad to each of them. The spiracles are in the center of these knobs. When the larva is mature, the flat disk develops into a conical cap and each of the knobs breaks up into two parts, thus making four all together on each cap surrounding a large round pit in the center. There are four curved grooves around these knobs (Plate LIV, 7), distinctly delimiting the discontinuation of the chitin at the tip of the cap. The central pit is bordered with four fan-shaped chitinous membranes which Trägårdh calls " chitin blätter." These membranes are outspread when the caudal tips come to the surface for breathing, but each becomes folded longitudinally to cover over its spiracle when immersed.

Each dorsal trunk has eight pairs of inner branches and ten pairs of outer branches. The former are smaller than the latter. The branches of the first pair at the fourth body segment of the larva attach to each side of the cephalopharyngeal skeleton and there ramify. The branches of the second pair originate in the same segment, and shortly after their origin each branch divides into an anterior and a posterior sub-branch, the former going to the cephalopharyngeal mass, the latter to the ring. The third and fourth pairs are found in the fifth and sixth segments, respectively, overlying and supplying the proventriculus. Branches in each of these two pairs meet each other and are conjoined at their tips, thus resembling a commissure. Following this are the fifth and sixth pairs in the sixth and seventh segments, respectively. These supply the posterior part of the proventriculus. The seventh pair lies in the eighth

segment, and, as with the third and fourth pairs, the tip of each branch from one side meets its fellow from the other to form a false commissure. Finally, in the tenth segment is the eighth pair. Both this pair and the preceding one supply the convoluted mid-intestine.

Of the outer branches, those of the first pair arise in the fourth segment. They turn inward, extend forward as far as the first segment, and divide into several branches there to supply the muscles of the cephalopharyngeal skeleton. In the fifth and sixth segments arise, respectively, the second and third pairs, which supply the imaginal disks of the wings, halteres, and mesothorax. These branches divide into sub-branches. The sub-branches of the second pair go to the third segment and end underneath the cephalopharyngeal skeleton, either with or without further ramification. The sub-branches of the third pair are connected with different structures within the body cavity. One of the sub-branches of this pair connects with corresponding tracheal branches of other segments to form the slender ventral trunk. From the fourth pair to the eighth, inclusive, each branch consists of four sub-branches, one arising from the dorsal trunk, one going to the ventral trunk, one penetrating the fat bodies and ending in the dorsal body wall, and one passing mesad underneath the dorsal trunk and supplying the alimentary canal. In the sixth pair there is a prominent white tracheal body in each inward-turning sub-branch. The function of these bodies is perhaps hydrostatic. The ninth pair is similar to any of the preceding ones, except that one of the sub-branches, instead of attaching to the alimentary canal, goes to the lateral body wall. The branches of the tenth pair are very strongly developed. They arise in the caudal process and extend forward as far as the eighth segment, to connect with the alimentary canal. Each branch has two large sub-branches, one anterior and one posterior. The anterior sub-branch goes to the eleventh segment and is attached to the hind intestine. The posterior sub-branch subdivides itself again, sending out an anterior sub-branch to supply the twelfth segment and a posterior sub branch to extend to the end of the caudal process. The strong development of the last pair of the outer branches, as Trägårdh considers, is due to the elongation of the hind intestine, but, in addition to this, the writer is inclined to think that the elongation of the caudal process, when the larva grows, must be a cause also.

In the dorsal trunk taenidia are present in the parts anterior to the first outer branch and posterior to the sixth outer branch. These parts are distinguished from the rest by the dark brown color. In the parts where taenidia are absent the color of the tracheal trunk is silvery white. There is an absence of taenidia in four places in each trunk, three of which are close behind the sixth, seventh, and eighth outer branches, respectively, and one is between the ninth and tenth outer branches.

As already mentioned, the ventral trunks are a secondary make-up through the connection of the sub-branches from the dorsal trunks, so they are much more slender and delicate than the dorsal. In each trunk the anterior end ramifies in the fourth segment underneath the cephalopharyngeal skeleton. From the fifth to the eleventh segment, inclusive, there is an inner branch in each segment. This inner branch ramifies in the prolegs. In the twelfth segment the anterior end of the trunk ends with the alimentary canal. The ventral trunk has two outer branches in each segment from the fifth to the tenth, inclusive. All of them go to the latero-dorsal body wall (Plate LIV, 8 and 9).

The fine branches that penetrate the subesophageal ganglion are connected with the ventral trunk. Such connection can be best seen from the lateral aspect, when the specimen is fresh and the trachea are filled with air.

The nervous system.— The nervous system of this form in general differs very little from that of the larva of Musca. The nervous center consists of a boat-shaped ganglion and two prominent cerebral lobes. Between the latter pass the esophagus, a pair of tracheae, and the dorsal vessel. Cephalad to the lobes are two major cephalic imaginal discs, each of which is connected antero-laterally with an optic stalk. The only difference here from the larva of *Musca domestica* is that there is no such problematical cellular structure as was figured by Hewitt (1908), situated close above the major cephalic disks and the cerebral lobes (Plate LIV, 10).

The nerve branches I and II arise from the cephalic part of the central ganglion, one of them (I) going to the cephalopharyngeal mass, and the other (II) going to the muscles of the lateral pharyngeal sclerites. There are three pairs of nerve branches (a, b, and c) arising from the stalks of the prothoracic and mesothoracic disks. In addition to these, nine pairs arise from the lateral and caudal parts of the ganglion. From

the posterior half of the central ganglion arise three unpaired accessory nerves which are much finer than the others. Except in the first four branches (I, II, a, and b) the bifurcations of these nerves are very similar to that in the Musca larva, while in innervation there is practically no difference between these two forms (Plate LV, 13). Each of the fourteen paired nerve branches is associated with a trachea (Plate LIV, 10). The penetration through the ganglionic sheath by the trachea gives a metallic luster along the edge of the ganglion.

There are two prominent pairs of sense organs in the head region. The anterior pair is on the antennae and the posterior pair is on the maxillary palpi (Plate LIV, 2). The palpi are shorter than the antennae, are not jointed, and have a broader base. The innervation of the former comes from the subesophageal ganglion (Trägårdh), that of the latter from the cephalopharyngeal mass. On the dorsal and lateral parts of the thorax, and along the lateral of the entire abdomen, parallel to the main tracheal trunks are papillae of another type which are much more slender, with a cylindrical stem. At the tip of the stem branch are three or four tentacles. These have been figured by Trägårdh (1903). The nerve ganglia lie close above the upper pharyngeal plate. They are fused anteriorly but clearly separated from each other behind. These are the epipharyngeal ganglia. Just opposite to them, on the ventral side of the pharynx, are the hypopharyngeal ganglia. These two pairs are best seen in cross sections.

The muscular system.— The muscles, aside from those of the alimentary and vascular tracts, are in two main groups—one controliing the cephalopharyngeal region, the other constituting a part of the body wall. It is these two main groups of muscles which are herein discussed.

The cephalopharyngeal muscles.— In the cephalopharyngeal region the muscles are very similar to those found in the larva of Musca. Starting from the cephalic end, a pair of mandibular extensors is seen, inserted on the dorsal side of the mandibular sclerites. The attachment of these muscles is made to the dorsal body wall of the third segment. Caudad to these another pair of muscles is inserted on the dental sclerites. These are the mandibular depressors. The other end of this pair on each side is divided into three bands and attached to the ventral process of the lateral pharyngeal plate. On the hypostomal sclerites are inserted four pairs of muscles, two dorsal and two ventral. The dorsal pairs are attached

to the intersegmental ring of the third and fourth segments, while the ventral pairs are attached, one to the caudal end of the dorsal process of the pharyngeal plate, and the other to the ventral. They are stomal dilators. The pharyngeal depressors are the pair of muscles situated dorsal to all the others. They have one end attached to the intersegmental ring between segments 3 and 4, and the other end inserted on the posterior end of the dorsal side of the pharyngeal mass. There are two pairs of cephalopharyngeal protectors, one dorsal and one ventral. These are attached to the third segment of both the dorsal and the ventral side, respectively. Their other ends at each side are inserted together on the dorso-lateral region of the posterior end of the pharyngeal mass. Six pairs of cephalic retractors are inserted into the cephalic ring between the first and the second segment. The three dorsal pairs are attached to the posterior end of the fourth segment, while the three ventral pairs, attached to the same segment, are slightly cephalad in position.

Within the pharyngeal mass there are two sets of muscles, which are best seen in sections. One set is longitudinal. Hewitt, in the Musca larva, calls them the *oblique pharyngeal muscles*, because their ventral attachment is posterior to the dorsal attachment. These muscles are attached dorsally to the inside of the dorsal ridges of the lateral plate and ventrally to the roof of the pharynx. The other set is best seen in the caudal region of the pharynx. They lie horizontally over the pharyngeal cavity, and are called by Hewitt the *semicircular pharyngeal muscles* (Plate LV, 20).

The cutaneous muscles.— On the inner side of the dorsal body wall, two pairs of the dorsal longitudinal muscles are found, lying on both sides of the median line. They are arranged according to the body segments. On the ventral side there are three pairs of ventral longitudinal muscles. Both the dorsal and the ventral sets are the most prominent muscles of the body wall. Between each two segments, from the fourth to the twelfth inclusive, a more or less spindle-shaped muscular band, called the *intersegmental muscle*, touches both the dorsal and the ventral longitudinal muscles. There are two pairs of lateral longitudinal muscles on both sides which extend from the third segment to the twelfth. The more ventral muscle on each side comes anteriorly into contact with the cephalic retractor in the fourth and fifth segments but turns away before it terminates near the demi-annular muscles in the second segment, while

the more dorsal muscle comes anteriorly to the third segment and ends almost in the same region as does the ventral muscle. All these muscles in the two pairs come posteriorly into contact with the ventral longitudinal at the posterior end of the twelfth segment. The oblique muscles are separated in each segment, from the fourth to the twelfth. In each segment there are three pairs of internal dorso-lateral oblique muscles and three pairs of external muscles. Likewise, there are both internal and external ventro-lateral oblique muscles, but only one pair of each. Two pairs of internal ventral oblique muscles and one pair of external ventral oblique muscles are found in each abdominal segment except the twelfth. The demi-annular muscles are found in each segment. There are four pairs in segments 5 to 11, inclusive, while in the other segments the number varies. In the last segments the muscles that are connected with the anal lobes are the anal muscles (Plate LVI, 31 and 32).

The alimentary system.— The alimentary system consists of the tract and its appendages. The alimentary tract in the mature larva is about three times as long as the entire body. The different parts of the tract are distinctly marked out by constrictions or by the insertions of the appendages.

The mouth opens ventrally at the anterior end, bordered by two oval lobes. The mandibular sclerites are exposed, each bearing a series of "teeth" resembling a comb. The hyposternal sclerites are set posteriorly inside the oval cavity, but they are invisible through the semi-transparent skin. Four pairs of large chitinous tubercles are arranged in two series close beside the oval cavity, and lateral to them are four series of smaller ones. Their size increases to the last row. At the farthest cephalo-dorsal position are four large tubercles, two on each side of the median line, and still dorsad to these, another four large ones are found close to one another in a row, resembling the premaxillary teeth of the mammals (Plate LV, 15).

The cephalopharyngeal skeleton.— In the second instar the "skeleton" is very slender. The mandibular sclerite consists of a single piece, more or less U-shaped and with a series of teeth, while another single piece composes the remainder of the skeleton. These two pieces of the whole skeleton are rather apart from each other but joined with each other through muscles. As the larva matures, the U-shaped piece breaks into two pieces. Dorso-caudad of them are a pair of dental sclerites and a pair of slender chitinous plates. A pair of hypostomal sclerites are

separated from the rest of the skeleton. These sclerites are connected ventrally by a hypopharyngeal sclerite. The rest of the skeleton is divided into dorsal and ventral lateral plates. Each has a caudal process projecting posteriorly. The dorsal and ventral plates are connected with a dorso-ventrad piece, making an I-shaped outline (Plate LV, 19). At the anterior end of the dorsal plate lies the epipharyngeal sclerite. The caudal part of the ventral lateral plate is broad but gradually thins away. Near the dorsal angular border of this plate an oval opening is often found.

The pharynx, as in the larva of Musca, has eight grooves separated by the bifurcating ribs at its floor. These ribs, differing from those found in the Musca larva, are rather Y-shaped, with fine comb structures at the tips of the upper processes. This evidently suggests a straining function. The loose membrane attached to the layer of cells covering the lateral plate, found by Hewitt in the Musca larva, is also found here (Plate LV, 19).

The esophagus is uniform in diameter throughout its length. It passes through the foramen between the cerebral lobes and the subesophageal ganglion, leading posteriorly to the proventriculus (Plate LV, 14), with which it communicates by means of the esophageal valve.

The proventriculus has very thick epithelium and its shape is more or less oval. As the posterior esophagus telescopes into the central core of the proventriculus, the large, clear cells of the proventriculus surround this inserted part. At the anterior part of the proventriculus and at the posterior end of the esophagus the epithelial cells are very large.

The chyle stomach may be divided into two parts. The narrow anterior part is the ventriculus, while the broader posterior part is the mid-intestine. The convolution of the chyle stomach is very complex. The anterior end, where the four caeca arise, is the broadest part in the entire alimentary canal. The epithelial cells of the ventriculus are large. The striated appearance, as in the other dipterous larva, is found on the sides of cells facing the lumen. The mid-intestine has a very thin epithelium and the wall of this part in the alimentary canal is almost transparent. The lumen, of course, is much larger than in the ventriculus (Plate LVI, 25).

The hind intestine begins with a very narrow part, then it broadens, but as a whole it is much narrower than the chyle stomach. It curves immediately after it commences, at the place where the malpighian tubes

arise, and then runs posteriorly toward the last segment. The epithelium in this part becomes thick again. At the tenth and eleventh segments it becomes narrower, and then begins the rectum (Plate LV, 14). The rectum has a very thick muscular wall. The chitinous intima is thick. As the anal opening is ventral in the twelfth segment, the position of the rectum is almost vertical.

The appendages of the alimentary canal.— The salivary glands are large and tubular. Each one has a narrow duct leading to the pharyngeal mass, under which the two ducts unite into one. This common duct leads forward and opens into the pharynx (Plate LV, 14).

The four caeca, attached immediately behind the proventriculus, have a broad base and each is glandular in appearance (Plate LV, 14).

The malpighian tubes are very large and often twisted among the convolutions of the alimentary canal and the large fat bodies in the abdominal region. There are two pairs, and each pair has a common root inserted at each side of the end of the mid-intestine. The tubes consist of large cells with prominent nuclei (Plate LVI, 26).

The vascular system.— The dorsal vessel consists of the heart, which is posterior, and the aorta, which leads anteriorly from the heart. This vessel lies immediately beneath the skin and above the alimentary canal and the four large fat bodies. The heart is the swollen and enlarged part lying in the last four segments. The anterior end of the dorsal aorta is between the cerebral lobes of the brain. The heart has three pairs of ostia situated latero-dorsad. They are furnished with valves which lead from the body cavity into the heart. Immediately at the anterior end of the heart there is another pair of valvular flaps regulating the flow of blood into the dorsal aorta. Along the sides of the heart and attached to the ventral side of it are three pairs of wings. Each wing has its narrow tip connected to the lateral body wall. The pericardium, which forms a narrow sheet along each side of the dorsal vessel, extends through the entire length of the heart and a part of the aorta. The extension can be readily recognized through the large epithelial pericardial cells. These cells are arranged one after another at short intervals along the dorsal vessel. The muscles in the wall of the dorsal vessel are arranged transversely and longitudinally, but chiefly in the latter direction in the aorta, and almost exclusively in the heart. At the posterior end of the heart extend three more wings, two lateral and

one dorsal; the dorsal wing is attached to the dorsal body wall, while the two lateral wings are attached to the lateral body wall. These wings are, however, smaller. The pericardium is profusely supplied with tracheae (Plate LVI, 33), as has been found in other dipterous larvae, such as Musca, Calliphora, Psychoda, and Anopheles.

The reproductive system.—In the mature larva a pair of gonads is found in the fifth abdominal segment. They are imbedded in the fat bodies and each has its duct leading posteriorly to the ventral body wall. They are pyriform, and at the posterior end there is an accumulation of imaginal disks. The general arrangement of cells in the gonads (Plate LVI, 34) is similar to that described by Weismann (1864) in the larva of *Musca vomitoria*, and according to his description these gonads are a pair of testes.

The imaginal disks.— The imaginal disks in the larva are of two kinds, the paired and the unpaired. The latter are insignificant and developed later, while the former are prominent and perfect in shape as soon as the larva enters the third instar. The unpaired disks are found in the alimentary canal and in the hypodermis, and they have to do with the development of the future fly. The writer has not been able to find the hypodermal rudiments in his preparations, because they are developed after pupation commences. Those scattered in the alimentary canal are similar in shape to those found in the larva of Musca. They are located at the anterior end of the proventriculus, all over the mid-intestine, behind the base of the malpighian tubes, surrounding the anus, and at the anterior end of the salivary glands, as figured by Kowalevsky (Plate LV, 14). The paired disks may be again divided into two groups according to their locations, namely, the cephalothoracic and the abdominal disks.

The cephalothoracic disks.— There are eleven pairs of disks in this region. They are the centers of development for the different parts of the imaginal head and thorax, and their appendages. Closely adjacent to the cerebral lobes is the pair of optic disks, which are connected with the lobes through the optic stalks. The optic disks are applied to the front of the lobes with their posterior concave surface, while their anterior convex surface is connected with a stalk leading to the antennal and frontal disks. The two pairs can be distinguished in sections. The antennal disks, more or less elliptical in outline, lying between the optic disks and the cephalopharyngeal skeleton, terminate in elongated stalks,

leading cephalad to the pharyngeal skeleton (Plate LVII, 35). Ventrad to these two pairs just mentioned are two other pairs; the pair situated near the central ganglion are the mesothoracic disks, which will be developed as the mesothorax and the middle pair of legs, while the other pair anterior to them are the prothoracic disks for the prothorax and the anterior legs (Plate LVII, 36). These latter two pairs are similar in shape to each other, each having an elongated stalk leading out forward and connected with the ventral hypodermis. There are four pairs of disks on the dorsal tracheal trunks (Plate LVII, 37). In each trunk close behind the prothoracic stigma is the stalkless, and more or less bean-shaped, pronotal disk embracing the tracheal stem (Plate LIV, 6). In the fourth segment is a disk, the largest of all, known as the *mesonotal and wing disk*. This disk is somewhat pear-shaped, is connected with the tracheal trunk, and has its stalk leading forward. Mesad and ventrad to this are two smaller disks. The anterior one is the mesothoracic disk, and the posterior is the metanotal and the haltere (Plate LVII, 38). To the external side of the hypostomal sclerite is attached an oval disk (Plate LVII, 37), and another is attached to the internal side of the sclerite. The former is the proboscis disk, and the latter the pharyngeal, which can be best seen in sections. Hewitt maintains that the maxillary disks are small and flask-shaped, and are found at the base of the oval lobes, but the writer is inclined to think these are probably a pair of sense organs.

The abdominal disks.— Closely ventrad to the rectum is a pair of pear-shaped disks which have been considered as the rudiments of the external genital appendages. Differing from what has been found by Künkel d'Herculais (1875) in Volucella, the other pair is absent (Plate LVII, 37).

The peripodal membrane is thin and transparent. When pupation commences, the differentiation of these rudiments can be seen through this delicate envelope. Each of the stalked disks has a nerve branch and a fine trachea. The parts that are sheathed within the peripodal membrane can be readily recognized (Plate LVII, 39 and 40).

Growth

Molting

While making observations on the development of the larva after hatching, molting has frequently been noticed. As soon as the young larva attains its size, about three millimeters in length, the skin splits

longitudinally along the dorsum of the second and third segments, and through this dorsal opening emerges the head of the larva of the next instar. The rent here may become much enlarged, extending backward as far as the sixth segment, while the larva is struggling for liberation. It seems that the larva does not encounter much difficulty in slipping out of the old skin. Because of its cylindrical body and short prolegs its escape is easy. Sometimes, however, the last pair of prolegs causes a great deal of trouble. These prolegs are often caught on the cast skin with their claws. After a struggle, lasting sometimes for half an hour, when the caudal processes have been pulled out, these remain still entangled with the cast skin. The larva, as it has sometimes been observed, twisting and bending its body, uses its mouth parts to bite this off. In the exuviae are found the entire cephalopharyngeal skeleton, part of the alimentary tube, and the tracheal trunks from out the caudal processes.

The writer did not observe the second molting. A premature molting may be caused by subjecting the larva to certain abnormal conditions, as once it was done by accidentally dropping larvae in kerosene. Such a molt, however, is quite different from an ordinary ecdysis; it consists of nothing more than the primary cuticula, and the structures that are cast off sometimes with the ecdysis are not to be found in it.

Instars

The first instar.— The newly hatched larva measures from 1 to 1.5 millimeters in length. The body segments are very distinct but the caudal processes are just budding out. At their blunt end are chiefly visible the tracheal terminals. These terminals are much simpler than those found in a grown larva, each having an opening, laterad to which are two roughly outlined bullae. Of the anterior spiracular processes there is not a trace to be recognized during this stage. The cephalopharyngeal skeleton is delicate and slender in shape, consisting, at the anterior end, of a single piece of U-shaped mandible sclerite and, following this, a pair of H-shaped structures, representing the hypostomal sclerites in front and the lateral pharyngeal plates posteriorly. The mandible sclerite and the rest of the cephalopharyngeal skeleton are apart from each other, but they are connected and articulated with each other by muscles. The alimentary canal is a more or less straight tube and

the salivary glands are relatively large. This stage lasts from four to five days at a room temperature of from 23° to 35° C.

The second instar.— At this time the larva is provided with a pair of pale, slender, anterior spiracular processes, the digits of which are short and not distinct. The posterior spiracles have assumed the general shape that they will have in a full-grown larva, but are smaller in size. Each of them has a chitinous cap with an opening at the center, surrounding which are four tubercles. The cephalopharyngeal skeleton is much thicker and heavier than in the preceding stage, and the hypostomal sclerite is now a separate piece from the lateral pharyngeal plate. This stage lasts about four days at a temperature of from 25° to 28° C.

The third instar.— The larva has attained its maximum size of from 12 to 13 millimeters in length. The difference in body structure has been described under *Morphology*, page 567. The larva completes its development and pupates in the course of three or four days at a temperature of from 29° to 30° C. Sometimes under less favorable conditions this stage may extend over a period of about a week.

Observations on growth in salt and fresh water

The following experiments were performed in the laboratory. Each aquarium was 5.5 centimeters in diameter and contained water, salt and fresh, with a depth of about 1.25 centimeters. Water and food materials were added whenever necessary. The aquaria were in series, placed near a window and carefully guarded against dirt and accident.

Experiment I.— Three larvae, each of which measured from 2 to 2.5 millimeters in length, were placed in salt water. After four days they measured 5 millimeters each; after five days one of them measured about 7 millimeters and the other two about 6 millimeters; after seven days the largest one measured 9 millimeters; after eleven days the largest larva pupated, while the other two measured 9 and 7 millimeters, respectively; two days later the remaining two larvae pupated. The room temperature ranged from 23° to 29° C.

Experiment II.— Three larvae of the same size as those used in Experiment I were placed in fresh water. After four days each one measured about 4 millimeters; after five days they averaged from 4.5 to 5.5 millimeters in length; after seven days one measured 7 millimeters and died, while the other two measured about 6.5 millimeters on the tenth day

and died. The average room temperature was the same as that in Experiment I.

Experiment III.— Four eggs were placed in salt water. After one day one of them hatched and the larva measured 1 to 1.5 millimeters; later on the same date the remaining three eggs hatched and on the fifth day the larvae averaged from 4 to 5 millimeters in length; after seven days they averaged from 7 to 8 millimeters; after eleven days one larva measured 10 millimeters, a second one measured 9 millimeters, and the other two measured from 8 to 9 millimeters and at this time pupated. On the thirteenth day the other two pupated. The average room temperature was the same as that used in Experiments I and II.

Experiment IV.— Four eggs from two to three days old were placed in fresh water. After one day two of them hatched; after four days these two larvae measured from 2 to 2.5 millimeters each; after five days one measured 3 millimeters, and the other 4 millimeters; after seven days the other larvae, which hatched out much later, averaged 2.5 millimeters each; the one which measured 4 millimeters on the fifth day died. All the others died on the thirteenth day. The average room temperature was the same as that in the first three experiments.

In a comparison of the results of the above experiments, the striking difference in the development of the larvae in the fresh and in the salt water may at once be seen. None of the larvae could grow well and attain pupation in the fresh water with the total absence of salt, although other conditions were equal. The larval stage in salt water, under the conditions previously stated, lasted from eleven to thirteen days. The pupation took place much earlier than usual, when the larva was only from 8 to 9 millimeters long. This was, perhaps, due to the more even temperature or other artificial conditions maintained in the laboratory.

Habits

Locomotion

The larvae are always found in still and stagnant water. Their modes of locomotion, under normal conditions, show their adaptation to such environments. First of all, the larvae are slow in movement, never darting nor jumping with appreciable speed; in the second place, they are awkward in directing themselves forward and turning themselves around, never exhibiting any energetic directness. And finally, the larvae, especially when reaching maturity, prefer to remain still on

rocks, logs, or floating leaves near the surface for a considerable length of time, without attempting to make a change in place unless compelled. The locomotion may be classified into four modes.

Crawling.— As the body is more or less cylindrical and smooth, and not equipped with specialized organs for swimming, the larva crawls most of the time at the bottom or on some object floating in water. Its prolegs, although short, are equipped with well-developed claws for such a purpose. In the summer season, when it is cloudy, a number of larvae are often found crawling slowly on floating logs in the pools or on the soft mud bottom in the shallow, seldom disturbed water of the overflowed areas. The larva, in its way of progression, much resembles a caterpillar, only that its prolonged caudal process is held upward like a cat's tail, waving around, and sometimes even bending forward to touch upon the dorsum. Under bright sunshine, by the sudden brushing away of the floating scums, the larvae hiding in the shade beneath are put to "flight"; however sluggish they seemed, they now begin to crawl faster, showing uneasiness under the suddenly changed conditions. This, of course, can only be attributed to the effect of light, which will be discussed later. The larvae — most of them mature — have been found crawling on floating scums. In the laboratory aquarium the writer has seen a young larva crawl into an algal mass, become trapped with the filaments, and then struggle for freedom; being tangled with algae on the claws of its proleg, the larva was deprived of liberty, yet, because there was abundant food material in such a mass, it probably did not die, but attained maturity.

Swimming by means of wriggling.— Wriggling is another mode of locomotion generally employed by the larva. The body of the larva is not slender, consequently its wriggling is not so rapid and vigorous as that in some other aquatic dipterous larvae. But this larva, nevertheless, bends and twists itself freely in all directions. Its caudal process, naturally, is the most flexible part, whipping and lashing around to help in locomotion. It wriggles sometimes near the surface, sometimes near the bottom, or sometimes between the surface and the bottom, in no definite direction; but more frequently it ascends and descends in the water. After a shower or in the late afternoon of a clear day, a number of the larvae may be seen wriggling very slowly, each with one side of the body upward about an inch below the surface in open water. In wriggling, as well as in crawling, two or more larvae sometimes hold together by

means of the last pair of prolegs, or with the prolegs of one on another part of the other, entangled and struggling aimlessly.

Floating.— The larva often floats itself up to the surface. The larva does not necessarily touch the surface, but often stays about an inch below. Usually, when floating, the larva has its head pointing obliquely upward and its body held, bending or straight, in a somewhat horizontal position. However, there is no definite rule as to its position.

Dropping.— Dropping may take place after wriggling, after staying below the surface for a considerable time, or immediately after floating. Sometimes the larva, instead of holding its head obliquely upward as it often does, reverses the process in making its way downward. In pools I and II, where the water is clear, this mode of locomotion can be best observed when the larva is getting near the bottom. Its body seldom touches the bottom, for at some point within an inch from the ground the larva will stop dropping and remain stationary. Sometimes wriggling may be assumed at this moment. Likewise, wriggling may also break in midway in dropping, so this mode of locomotion is likely to be interrupted almost anywhere before the end of the descent is approached

Feeding

Method of feeding.— The larva often crawls on the surface of floating leaves and stops there to feed. Its mandibular sclerites move rapidly, bending back and forth. The head segment is extended and moves with frequency, corresponding to the movement of the cephalopharyngeal skeleton. The mouth parts graze vigorously on the materials deposited on the plant surface, and the tooth-like structures on the ventral side of the distal part of the mandibular sclerites comb up the desirable materials. As the larva seldom feeds long on one spot, its head swings freely in all directions seeking a new feeding place. While the larva is feeding at the surface of open water, the ventral side of the first segment, including the mouth, is flatly applied to the surface film. The continuity of the latter is frequently disturbed by the vibration of the oral lobes. These lobes with their chitinous tubercles serve as a sort of brush in producing little whirling currents, in which the microscopic organisms are involved and brought to the mouth. Meantime the inner, more prominent tubercles, which are situated close to the oral cavity, sweep simultaneously toward the center. The mandibular and dental sclerites move forward to meet the flowing currents, and repeatedly relax and fall

back. This movement is carried on with great frequency, about two hundred times a minute. The current, which carries food materials into the alimentary canal, can be seen through the semi-transparent skin. A number of air bubbles move along in the convoluted tract. The larva also crawls in the dirt at the bottom, picking up food materials from the bottom surface and selecting them from within the mud.

Selection of food.— The food of the larva consists, in the main, of microscopic organisms living in the salt water. The green and yellow tinge in the pools, and the brown scums in the overflowed areas, are the chief natural sources from which the larva selects its food. Aldrich thinks that an alga of the Nostoc group, which is common everywhere in Great Salt Lake, often forming rotting deposits, must be the food of the Ephydra group. In the pools where these observations were made, no Nostocs have ever been found, but algae of other groups, green and brown, are found in considerable quantity. In the old pools, in which there is now very little salt, masses of Ulothrix float in the water. These plants probably furnish both shelter and food for the larvae. Evidently the larvae do not live on one particular kind of plant material. Besides algae, some decayed leaves, fragments of decayed grass stems, boards or logs, even some microscopic animals, such as Protozoa and bacteria, may be consumed by the larvae. Besides organic food, some inorganic substances, although undesirable, may get in the alimentary canal, without being digested. In studying the food selected by the larvae, twenty alimentary canals have been dissected and examined in the field under the microscope, and also in the laboratory immediately after the specimens were brought in. The materials constituting the stomach contents, that are recognizable and identifiable, are listed as follows:

	Specimens																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Cinders	...	...	c	...	...	c	...	...	vc	s	c	...	...	c	c	c	c	...	c	c
Iron rust	...	...	c	c	...	c	...	...	vc	s	c	...	...	c	c	c	c	...	c	...
Bacteria	...	...	...	...	...	...	...	...	...	...	...	vc	...	...	...	...	c	...	...	...
Pandorina	...	...	...	...	...	...	...	...	...	s	...	...	...	...	...	...	...	...	...	...
Vorticella	...	...	c	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Mastigophora	...	...	...	...	...	...	...	...	s	...	...	...	...	...	...	...	...	...	...	...
Gloeocystis	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	s
Astasia	...	...	...	...	...	...	...	c	...	...	...	...	...	...	...	...	...	...	...	...
Infusoria	s	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Synedra	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	s	...	...	s
Chlamydomonae	c	c	c	c	c	c	c	...	c	s	c	...	...	c	c	c	s	...	...	...
Navicula	vc	c	c	c	c	c	c	c	vc	vc	vc	c	c	c	c	c	vc	vc	vc	vc

c, Common; vc, very common; s, scarce

In addition to the natural materials selected by the larvae, different kinds of foreign food — foods not found in their natural habitat — were used to learn what kind of plant materials would serve as the most favorable food to them. The water taken from the pools was filtered in order to eliminate any natural food. The four kinds of foreign food — (1) cornmeal, (2) green grass, (3) broad leaf plantain, and (4) alfalfa meal—were placed respectively in four aquaria. Each aquarium had five larvae measuring from 7 to 8 millimeters in length. After five days the larvae in the first two aquaria all died. After two weeks, two pupae were found in each of the other two aquaria. At the end of three weeks, three adults and one pupa were found in the fourth aquarium with the alfalfa meal in the water.

Respiration

In respiration the larva sticks out its caudal process to indent the surface film. The spiracle membranes flatten out on the water surface, resembling the leaves of Marsilea, and the spiracles open to the air. Meanwhile the larva is feeding on plancton organisms, as indicated by the frequent moving of its mouth parts. After a while it withdraws its caudal tips from the surface film. It often requires considerable effort for the larva to pull them down into the water. Frequently the larva hangs suspended close underneath the surface, swinging its body back and forth trying to overcome the adhesion between the caudal tips and the surface film. The grown larva is able to relieve itself sooner or later, but to a comparatively young larva this attachment is a constant source of peril. On one occasion the writer found five young larvae, holding one another together with their last prolegs, hanging below the surface helplessly. In failing to swim they all died about a day later. The writer corked an eight-ounce bottle completely filled with salt water in which were a few larvae. A large air bubble was unavoidably left on the under surface of the cork in contact with the water. After five or six hours most of the larvae came up, getting around that large bubble, and remained there until they pupated. At another time several larvae were screened at the bottom of an aquarium, a piece of wire gauze being placed halfway between top and bottom; the larvae thus barred from reaching the surface were suffocated.

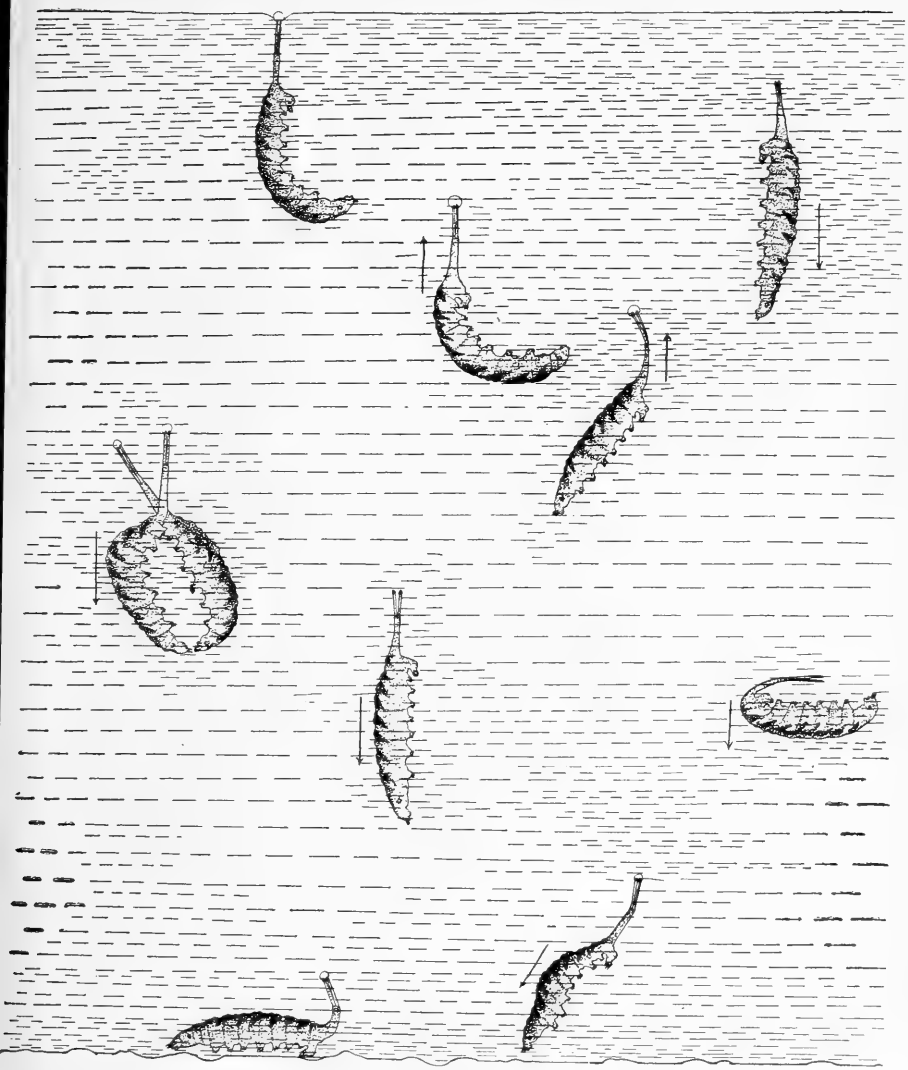

FIG. 73. RESPIRATION ACTIVITY

The writer observed the following interesting phenomenon relative to respiration. The water in the aquarium was thick with microscopic organisms and was greenish in color. Each of the several larvae crawling at the bottom had a bright silvery air globule attached to the caudal end. The size of that globule was as large as the head of the larva. Soon the globule became larger, and the larva floated up with it. As the larva touched the water surface with its caudal end, the silver globule suddenly burst and the larva immediately sank down to the bottom. Sometimes it took about ten or even thirty seconds for the larva to break the globule after it reached the surface. While the larva was in its course toward the surface, it lay straight, curled obliquely, or wriggled and clasped another larva with the last pair of prolegs. But whatever the position or movement the caudal end was always pointing upward. The air globule began to form when the larva was sinking down halfway or sometimes very near the bottom, and its size continued to increase thereafter. After the larva had crawled along at the bottom for about 5 or 6 centimeters, the globule gained its full size and the larva was ready to float up again (fig. 73). This rising and sinking of the larvae kept them restless and gave the aquarium a most lively appearance. It is believed that such action as this takes place only when the conditions in the aquarium are getting abnormal and unfavorable for respiration.

Preference for stagnant and shallow water

The conditions at the pools and overflowed areas are, throughout the season, admirably favorable to the life of the larva. It prefers stagnant water, because it wriggles and suspends itself under the surface, and, because of the absence of specially adapted apparatus, it is unable to gain foothold or to pursue its course in rapid streams. The larva prefers shallow water, because it is easy to reach the surface, where respiration takes place, and because the floating scums offer food supplies. The pools have no outlets, and the water, which is accumulated from rains in the summer season, remains permanently still and has never exceeded 40 centimeters in depth, so that the development of the larval life here is much favored. The presence of larvae in great numbers indicates that these pools serve as an excellent habitat. At different times of the season the salinity and density of the water vary greatly. Some of the pools have a sudden decrease of larvae owing to the over-increase

of these two factors, but the stagnant and shallow conditions, nevertheless, remain ever favorable to their life. The existing conditions at the overflowed areas, likewise, give a good evidence of the larva's preference in such a habitat. The water in these areas, like that in the pools, is always still and never more than 10 centimeters deep, and here are found the larvae in great abundance. Over the surface, thick brown scums for sheltering and feeding make another favorable addition for the inhabitants.

The running water in a narrow creek near this location has not been permanently inhabited by the Ephydra larvae. Once or twice, after several days drought, when the water was reduced to a low mark and became fairly stagnant at its shore, adults began to gather around and a few young appeared, crawling at the muddy bottom. But not long afterward, when a rain brought the water up to its original depth, flies were no longer able to alight on the surface and all the larvae disappeared in the rapid currents. In the pools, the ditches, and the overflowed areas at the salt works in Syracuse, similar conditions exist. At different points where the water runs in a low stream, some larvae were found drifting along without being able to make a stop or to direct themselves to shift to a favorable recess.

Preference for salt water

General range of percentages of salt in water.— Some marine animals placed in fresh water have their blood and body fluid disturbed through osmotic pressure; consequently death may ensue before osmotic equilibrium is established. On the other hand, if the percentage of salt in the water is greater than that in the animal's blood and body fluid, the same result also may follow. So neither hypertonic nor hypotonic solution is suitable for the larvae to live in, but between them there is a general range of percentages of salt that serves as an optimal medium. To this physiological factor is largely due the distinction in adaptation between the salt- and fresh-water animals. The fully grown larva of *Ephydra subopaca*, however, does not seem to be materially affected by either salt or fresh water. It is partly due to the circumstance that it has stopped feeding when pupation is imminent, and partly due to the condition of the body wall, which is gradually hardening to a puparium and has become impermeable. Thus the larva has been enabled, to a certain extent, to

stand the unfavorable external medium. In proving this the writer had several grown larvae kept in fresh water, which pupated afterward without difficulty.

Young larvae of the first and second instars, however, require salt water. None of the young larvae placed in a fresh-water aquarium for a period of three days survived, although food was provided. During the growing period the larva requires conditions near to the normal — that is, a range of percentages of salt in water, within which only a little osmosis takes place between the external and the internal medium. In solving the problem of that general range, four sets of experiments were performed.

In Experiment I, the young larvae were able to live in the water having low percentages of salt, while the older ones thrived better in the water of higher salinity. In Experiment II, most of the larvae could live in the salinities ranging from 1 to 8 per cent. Certain chemical substances dissolved in tap water may have had some effect, to a certain extent, upon the larvae, yet the results are plain enough to indicate their adaptability within a fairly wide range of different strengths of salt in water. In Experiment III, those larvae living in water having a salinity of from 1 to 9 per cent attained full growth and pupated, while those in a salinity of 10 per cent died one day afterward. The fact that 10-per-cent salinity is the maximal limit, beyond which no larva could live, is well shown in Experiment IV, even in the case of comparatively mature larvae. It is difficult to rear larvae of the first and second instars in salt water prepared in the laboratory; but in the water collected from the pools it can be done easily, even through all the stages of a complete life cycle. This difference may be due to the foreign food used, such food being less nourishing to the young larvae than the natural. And it is also due — perhaps chiefly — to the enriching nitrogenous substances brought to the pools through animal pollution. Such substances are entirely lacking in the laboratory aquarium. But in spite of these complications, most of the larvae did live and attain maturity within a general range of salinity of from 1 to 9 per cent, as shown in the four experiments.

Garrey (1904) says, "A dilution or concentration of the aquarium water always causes an equivalent in the blood of the invertebrates, and osmotic equilibrium between the 'external and internal media' is established." In the pools the salinity varies from time to time; rain often lowers it

and drought raises it. The adaptability to such wide range in salinity enables the larvae to survive in frequently changed conditions; and the frequent variation of salinity in the season favors the larvae in one way or another during different instars, and, as a whole, gives them plenty of chance to avoid fatalities.

Migration experiment.— The physiological significance of the larva's preference for salt water has been shown in the last paragraph. Such preference can be shown by its behavior equally well. On this an experiment was performed: In a metal plate having two series of compartments, each series was prepared as miniature aquaria by filling with fresh and salt water in alternate order. In each of the aquaria containing fresh water, six larvae were placed A narrow piece of cheesecloth was placed as a bridge between each two adjacent compartments, with each end reaching as far as the center of the bottom of each aquarium. The gentle slope along the cheesecloth immersed in the water afforded the larva a path for climbing over the bridge. Just one day after they had been placed in the aquaria fourteen of the twenty-eight larvae migrated to the salt water. Later the fresh water unavoidably became salty through the capillary action in the cheesecloth, but the rising salinity in the salt water was checked to a certain extent by a little fresh water being dropped in from time to time. Finally two larvae migrated back, while the other twelve remained. These observations are perhaps too few to warrant drawing conclusions, but it may be assumed that osmotic pressure acts externally and internally, and that it is a constant stimulus to the larva when it is subjected to a hypertonic or hypotonic solution. The larva is sensitive to such difference from the two media through contact with the external medium by its body wall as well as by its alimentary canal. Moreover, even within such range (1 to 9 per cent) as previously mentioned, in which the larva is able to live, there is still a further preference for percentage of salt as an optimal range for each individual larva, or at least for each instar, as shown by the larva's migrating back to the water with a salinity of 4 per cent from that of 8 per cent.

Factors influencing habits

Absence of air.— The larva is well equipped with particularly developed structures that enable it to stand some of the unfavorable conditions

to which it may be accidentally subjected. For example, the thickened, impermeable body wall of the mature larva, as already discussed, has enabled it to survive and attain pupation in water with a total absence of salt; the convoluted alimentary canal stores enough food for the larva in tiding over a period of starvation, when it happens to face scarcity of food in the water; and, likewise, the larva owes to its complex tracheal system its ability to stay at the bottom for a considerable length of time without obtaining air from the surface, when the conditions there are unfavorable and abnormal. The writer has not been able to observe the effect of total absence of air upon the larva, but inability to withstand deprivation of air has been tested in the following experiments, in each of which a glass relaxing jar 7 centimeters in diameter and 5 centimeters in depth was used as an aquarium.

Experiment I.— Four larvae were placed in water 40 millimeters deep, with a kerosene layer 5 millimeters thick. After twenty hours one larva was dead, and three were alive but moribund, and with air bubbles at the caudal tips.

Experiment II.— Four larvae were placed in water 40 millimeters deep, with a kerosene layer 4 millimeters thick. After twenty-two hours two were dead, and two were alive but moribund.

Experiment III.— Four larvae were placed in water 30 millimeters deep, with a thin kerosene layer. After twenty-four hours the larvae were all alive; after forty-six hours they were still alive but moribund, and some of them had air bubbles at the caudal tips.

Experiment IV.— Four larvae were placed in water 20 millimeters deep with a very thin kerosene film, barely enough to cover over the water surface. After twenty-four hours all the larvae were alive; after forty-six hours one was dead, and three were alive but moribund, and with air bubbles at the caudal tips.

In these experiments the larvae were deprived of a chance to come up to an open surface for respiration, and the air in the water underneath was very much limited in amount on account of the small volume of the aquaria. The great complexity and rich ramification of the tracheal branches must enable the larvae to store enough air to sustain their lives. The length of time through which they lived is directly proportional to the quantity of water from which they could gather dissolved air, and inversely to the thickness of the kerosene layer, which, though never

mixed with water, may contaminate it to a certain extent. The writer observed that when some larvae reached the top layer of the water, with their caudal tips in contact with the floating oil, they seemed to be repelled by it.

In the pools and overflowed areas the water often has greasy films spread here and there upon its surface, but there are enough exposed areas that give the larvae a chance to come up to the surface for respiration. Furthermore, the quantity of water underneath the films is sufficient to keep much oxygen in solution.

Temperature.— Throughout the summer the average temperature of the water in the pools is 25° C. Taking this temperature as a mean, the writer subjected the larvae to various thermal conditions in order to find out how high and how low a temperature they could stand. In an aquarium provided with suitable conditions, two larvae were kept in a temperature of from 27° to 28° C. They lived therein perfectly well. Feeding, wriggling, and crawling, as usual, they did not show any change in habit for fourteen hours. Afterward the observations were interrupted. The temperature was then raised to from 35° to 37° C. and two larvae were introduced into the aquarium, where they were found alive after eleven hours; but after nine more hours they died. When the temperature was raised again, wavering between 38° and 49° C., the larvae wriggled vigorously. Continuing to live for two hours, they were removed to another aquarium, in which the temperature permanently registered 42° C. There the two larvae died within thirty minutes. This experiment was repeated by placing two fresh larvae in a third aquarium in which the temperature varied between 40° and 44° C. These larvae died within one hour. In addition to this it was found that two grown larvae did not live longer than thirty minutes under a temperature of from 43° to 46° C. The writer concludes that a temperature of about 40° C. is the highest limit the larva can stand.

The larva exhibits a remarkable ability for enduring low temperatures. A larva was placed on ice for periods of ten, twenty, and forty minutes, and one hour, and at the end of each period was removed to water of ordinary temperature. However paralyzed the larva was while staying on ice, it would soon recover and become lively again after a few seconds. Mature larvae were kept on ice for twelve and twenty-four hours, respectively. Though they seemed dead while on the ice, each was found to

be alive when replaced in water of ordinary temperature. It is safe to assume that the larva can live in water at the freezing point for a still greater length of time, if no other detrimental factors are involved.

Light.— In order to minimize the influence of temperature, the experiment having to do with the effect of light was performed outdoors on a sunny afternoon in the latter part of October. The temperature on that afternoon registered 14° C. Twenty-two larvae were placed in a dish 14 centimeters long and 10 centimeters wide, containing water about 2 centimeters deep. A piece of board covering about two-thirds of the dish was laid over the top to produce a shade. Under bright sunshine the larvae had crawled around in water, but about half an hour after the shade had been placed over the dish, fifteen of the larvae came under the shadow. The board was then removed, and the dish was slightly jarred in order that the larvae might be evenly distributed. When the shade was again replaced, similar results happened within half an hour. This time six larvae were crawling in the light but all the others had gone into the shade. Then the dish was turned around and the formerly shaded part was now exposed to light. At the end of half an hour twelve larvae came quite to the end of the shaded part, two stopped at the middle, while the others were entangled together and with some plant materials in the water, and were moving back and forth at the border between the light and the shade. According to the behavior of the majority there seemed to be a general tendency among the larvae to evade light.

At noontime during midsummer the larvae living in the overflowed areas were found hiding themselves under the floating scums. In the pools they stayed at the bottom or at a considerable distance below the surface. This may have been due to the excessive heat from the direct rays of the sun so that light alone may not have been solely responsible. In the latter part of October, over a great part of the overflowed areas numerous larvae were aggregated along the side where the water was exposed to the morning sunshine, while at the other side, where the delta deposit produced an extensive shadow over the water, very few were found. The larvae were attracted probably by the warmer temperature in the morning, after they had endured a frosty night.

Desiccation.—The larva can stay out of water for a considerable time, provided the soil retains enough moisture. In midsummer, when hot

weather prevails, the water in the overflowed areas is rapidly diminished by evaporation and a great number of larvae are left on land. They sluggishly but steadily crawl about, seeking recesses in the soft mud. They come to some rocks, pebbles, sticks of wood, and the like, that are scattered here and there over the areas, and hide underneath.

Large numbers of larvae stay quite away from the shore, in the deeper water, and retreat with the receding water into deeper parts until finally the water is all gone; then they embed themselves in the soft mud and their dorsa are covered with dirt and scums. Such a covering is a great protection to the life of the larvae in dry weather. Two or three days after the water had receded, a larva was picked up from the mud or from the underside of a log or a rock and placed in water. It was found alive, crawling and wriggling as usual.

In midsummer, showers or gentle rains frequently flood the temporarily dried areas and the bottom mud becomes soft. Both the hidden and the embedded larvae begin to crawl, often producing long trails on the surface of the mud by the scratching of the last pair of prolegs of each larva. These trails are numerous, and are arranged irregularly and often of considerable length. They look like the prints made by pressing a bunch of twisted threads on the mud. In the laboratory some mud brought from the salt pools was entirely drained of water and a number of larvae were placed in it. They behaved just as those had done outdoors — that is, hiding themselves under pebbles and embedding themselves in the mud. Afterward, larvae picked up from the mud and placed in water were always found to be alive. At the end of the fifth day, they were found dead in the thoroughly dried mud. With such ability for resisting desiccation, the larva has much chance to get through a drought that does not last very long. The mud in the overflowed areas is always moistened by dews at night, and as long as moisture is present in the mud the larva will be able to live. Consequently, throughout the season very few larvae have been found killed by drought.

Gravity.— In summer and fall, when the larvae are active in swimming and feeding, they often float up to the surface and stay there for some time. They rise easily, but go to the bottom only with considerable effort. In the laboratory, when a grown larva is transferred from one aquarium to another it seldom goes to the bottom; it is often buoyed up again after it has been forced down.

In an aquarium with several larvae at the bottom, a piece of narrow board was placed at an angle of 60° with its upper end projecting slightly above the water. About an hour later two larvae had climbed to the top of the board, three were halfway up the board, and one was starting to climb. An electric light was then turned on and held about 13 centimeters directly above the water surface. All except one of the larvae started to go to the bottom. Then the light was turned out. At the end of an hour two larvae were climbing again, one of which was very close to the surface of the water. In repeating this experiment several times, whenever no light was hanging there the larvae steadily climbed toward the surface. Sometimes even after the light was turned on, they refused to go down but hid themselves in shade on the lower side of the board or under some floating leaves. The writer has frequently noticed that in the pools under the sun's direct rays the larvae hide themselves under floating boards, scums, and the like, in order to stay nearer the surface.

Mechanical injury.— The larva has been found incapable of regenerating any part lost from its proleg or caudal process. Cutting off the respiratory spiracles interferes with the normal process of respiration. Owing to the amount of air stored in the richly ramified tracheae, the larva is able to live for a short time. In one instance the larva died soon after one of the oral lobes was snipped off.

THE PUPA

Pupation and perching habit

When the larva is ready to pupate, it approaches some object and grasps an edge with its sixth and eighth pairs of prolegs. At this time it ceases its activities in feeding and swimming, the larval skin gradually hardens, and the wrinkles on it disappear. Its color becomes darker and darker, until it is homogeneously brown. The head region, including the first four segments, becomes depressed or slightly concave on the dorsal side and convex on the ventral side. Thus the outline resembles that of a shovel, but it is slightly narrowed toward the anterior end. The pupa perches rigidly on its support (Plate LVII, 43), secure for the transforming period. It is hard to remove it by jerking or shaking. A great number of pupae may be found perching side by side on a stick,

a cord, or any other object, either immersed in, or exposed outside of the water. All will, however, live through the transformation period. Failing to find any other object of attachment, a larva may grasp the dorsum of another larva's abdomen. Three or four, or even more, may so hold together and drift around in water.

The spiracles in the prothoracic stigmas and at the caudal tips are still functional after pupation has commenced, and continue so until the internal metamorphosis is completed, when the tracheal trunks become atrophied. The air stored within the puparium will be sufficient for the needs of the pupa for the time being. When the pupa matures and more air is needed, the adult will emerge.

The puparium is brownish, with pigmented spots on the dorsum. A well-pronounced edge is formed around the margin of the anterior end. The prothoracic stigmas now stand out laterally. Each is conspicuous with its four digits. The branches of the caudal process diverge laterally instead of pointing straight backward (Plate LVII, 42). When the pupa matures, its body contracts and separates from the wall of the puparium. The pupa is enveloped now in a transparent membrane. The head is broad, with two small antennal tubercles and well-shaped compound eyes. The proboscis is flattened in a truncate piece closely overlapping the coxae of the anterior legs. All three pairs of legs are closely pressed ventro-laterally. The wings are ensheathed by membranes, through which the convolutions of the veins are visible. Closely cephalad to the base of each wing there is a brown, knob-shaped spiracle (Plate LVII, 41).

Length of pupal period

The length of the pupal period varies greatly. The amount of food that the larva has taken before pupation, the location that the pupa seeks, temperature and moisture, rain and sunshine, and the salinity and the density of the water — in other words, both the internal and external conditions — have considerable influence upon the development of the pupa. Pupation records made in the laboratory are as follows:

Beginning of pupation	Emergence of adults	Number of days
June 29	July 10	11
June 30	July 6	6
July 26	August 4	9

Beginning of pupation	Emergence of adults	Number of days
August 2	August 4	2
August 4	August 13	9
August 8	August 13	5

According to the foregoing data, the length of the pupation period varies from two to eleven days. In the field, during hibernation, the period extends over four or five months.

Relation to environment

In different kinds of solutions

A number of pupae were kept at the bottom of a salt-water aquarium. Within ten days many flies emerged. The emergence of about the same number of pupae kept in tap water took place much later. In 5-per-cent formalin, adults emerged from the puparia floating on the surface, but in kerosene all the puparia sank to the bottom and none of the pupae developed.

When exposed to air

From the salt pools a stick of wood with numerous pupae attached was brought into the laboratory. Before the laboratory was reached, a few flies emerged. More continued to emerge in the laboratory before this piece of wood became entirely dry.

Effect of excessive heat

High temperature, within a certain limit, favors the development of the pupa and hastens the emergence of the adult. During the latter part of July the temperature in the laboratory registered about 30° C. The pupae kept in the laboratory did not show any unusual speed in development. After several days of sunny weather, the temperature rose steadily, registering between 39° and 40° C. at noon. Under each of three bell jars, from twenty-two to twenty-four half- or full-grown pupae were placed. At the end of the first day, from three to five adults had emerged in each jar; two days later the number had increased to six or eight; and at the end of the sixth day, to fifteen or twenty. This is assumed as the highest temperature the pupae could stand in the presence of plenty of moisture. In order that this assumption might be verified, the same

number of pupae were kept in bell jars in a greenhouse where the temperature registered 45° C. between 1 and 2 p. m. In this experiment all the pupae died at the end of the day.

THE ADULT

Emergence

The transformation to the adult stage was observed in the laboratory. The fly came out by breaking off the oval disk of the dorsum at the anterior part of the puparium. It struggled at the opening of the pupal case, but finally emerged without much difficulty. Each of its legs wrinkled like a French curve, and its ptilinum bulged like a glass globe. The ptilinum, with its somewhat pubescent surface, expanded and contracted at short intervals for about thirty minutes. The ptilinum then sank into the head, leaving a transverse cavity in the front. The sinking was gradual, and the ptilinum was pushed out again several times, but each time the pushing was weaker. Finally the cavity at the front was gradually narrowed to a very thin cleft. The fly moved around on the water surface and frequently rubbed its abdomen with its hind legs. About a quarter of an hour later it began to rub the tips of its wings. Through constant rubbings the wings began to expand at their tips, until they became straightened and entirely spread. The fly then gave a few more strokes and was ready for flight.

Food and feeding habits

The alimentary canals of ten flies were dissected and examined. The contents consisted almost entirely of Chlamydomona and Navicula. Bacteria, Mastigophora, and inorganic materials were found only occasionally.

Ephydra subopaca feeds in the same manner as does the house fly, but resting on water, on the floating scums, on leaves and the like, in the pools or on the surface of soft mud.

Preference for stagnant water

A calm water surface is most favorable for flies. They do not fly any considerable distance, and never higher than a foot above the surface;

neither do they hover over the water surface and dance in the air. Rapid streams are unfavorable to them, and they shun even slow-running currents. Because of the ripples at the shore, not a single fly was found in the lake, regardless of the proximity of the pools and overflowed areas.

Factors affecting the adult

Absence of salt in water

Unlike the larva, the adult does not require salt; it lives on the surface of salt water, but it lives on fresh water also. In the laboratory, adults were often confined on the surface of fresh water immediately following their emergence. Food was provided, and the flies lived, in most cases, from six to twelve days.

Heat

A newly emerged adult subjected to a temperature of 36° C. in the greenhouse died within three hours. A second one, kept in the same confinement but at a temperature between 25° and 26° C., lived until the next afternoon, when the temperature suddenly rose to 34°. The conditions here were, however, different from those outdoors. There was no shade for the fly to seek and no current of air, and the fly itself was deprived of liberty in changing from one place to another. Therefore in the field a temperature of 35° might not have affected it fatally.

Rainfall

Excess rainfall is beneficial to the adults in that it widens the water surface of the overflowed areas, maintains the normal salinity in the pools, and eliminates the chance for the loss of the natural habitat.

From the data gathered during the months of June, July, and August, in the two years 1916 and 1917, it was seen that the number of flies materially increased during the periods of greater rainfall.

Frost and snow

Unless frost is extremely heavy, it has very little effect on the adult flies. In September, when the frost was light there was not much change in the number of flies in the field; but later, when conditions were different, the following records were obtained:

November 1. Considerable frost; no dead flies found.

November 2. Considerable frost; flies very scarce in the pools, but numerous in the overflowed areas.

November 5. Very heavy frost and thin ice; flies on ice hardly able to move when turned over.

November 7. Heavy frost, and warm, bright sunshine; flies lively, staying on ice; six newly emerged flies and three mature flies died.

November 22. Frost and snow; two mature adults found; one newly emerged fly died.

November 28. Snow; no flies found.

Mating

Mating was observed on June 30. The male frequently jumped upon the female, trying to mate, but such attempts often resulted in failure, the female being unresponsive. He clasped the front of the female's head from behind with his front legs, while the middle legs held onto her mesothorax and his hind legs onto the posterior third of her abdomen. By holding her fast with the two anterior pairs of legs, his hind legs were then able to move freely, rubbing on the female's genitalia continuously for about thirty seconds. The female then turned the tip of her abdomen upward. The male's abdomen was held in its usual position while a slender and pointed penis was protruded downward and inserted into the genital opening of the female. Copulation thus took place and lasted about four or five minutes. Then the penis of the male was drawn out, exposed for a while, and was finally withdrawn into his abdomen. He remained on the female for a few minutes before jumping away, but at times the male has been noted to hold the female under his feet for more than an hour.

THE EGG

Oviposition

Oviposition seems to be a very brief procedure. The writer observed a single female oviposit seven times within twenty minutes. Each time a single egg was laid on the water surface by the female's merely touching the latter with her ovipositor. The eggs thus laid immediately sank to the bottom.

Description

The egg is elongated oval in shape and measures 0.9 millimeter in length. Both ends are practically equal in breadth and the egg is slightly

curved at the middle. The anterior end has a micropyle (Plate LVII, 44). The chorion is grayish white, but sometimes slightly pink. The surface is reticulated with hexagonal markings.

Hatching

The egg can hatch in salt water, in lake water, or in tap water. Temperature has marked influence on the development of the egg, for under a temperature of between 18° and 20° C., hatching did not take place until the end of the third day, while under a temperature of 33°, eggs began to hatch after seventeen hours but most of them were killed soon afterward.

As the embryo develops, the mouth and the claws of the prolegs are more or less visible through the chorion. The body is bent in the egg shell. The movement of the claws gives an appearence of wave motions. The mouth parts frequently gnaw on the inside of the chorion, producing a wedge-shaped transparent part. The head breaks the chorion and the opening is enlarged by the forcing-out of the thorax. While the body is wriggling outside, the claws of the last pair of prolegs often hold onto the broken edge of the shell. The larva must struggle before being freed. The emergence usually takes from thirty to forty seconds.

PROTECTION

Ephydra subopaca has several interesting characteristics that serve for protection throughout all the stages in the life cycle. First, it has protective coloration. The egg is grayish opaque and can scarcely be seen when at the bottom of the water; it is sometimes slightly pinkish and is thus more easily confused with decayed plant materials in the salt pools. While crawling in shallow pools, the larva gathers dirt all over its body, making it resemble the color of the muddy bottom and also that of the floating scums. When the larva is mature and ready to pupate, its hypodermis becomes hardened and gradually turns brown, resembling the color of the plant matter on which the pupa perches. The coloration of the adult, as has been described, harmonizes also with its background. Boards, logs, scums, or the surface of soft mud in the temporarily dried areas, with a number of flies scattered here and there, look concolorous—that is, uniformly dull brown; thus a swarm of flies can hardly be distinguished from a distance without careful inspection.

Secondly, the structure is a protective feature. The thick chorion of the egg, the thick hypodermis of the larva, and especially the hard skin of the pupa, enable the species to survive in a wide range of salinity and under various unfavorable conditions, and protect the insects from being harmed by mechanical means.

Thirdly, the habitat seems to be protective in character. As already mentioned, eggs laid on the water surface sink to the bottom, and thus are avoided certain catastrophes that might be caused by temperature, climate, or mechanical agents. Furthermore, eggs are laid singly. Being so minute in size, they are by no means easy to detect by any predacious insect in the pools. The larva has a hiding or shelter-seeking habit. The perching habit of the mature larva has made the animal most inconspicuous in its environment, and this is true also with the adult's habit of resting on water surface or on mud where the scums afford a harmonizing background.

Fourthly, the adaptability of the species to such a unique habitat is in itself protective. The salinity and density of the water unfit these pools as a habitat for most of the aquatic insects that thrive in fresh water. This keeps this species from contact with certain predacious forms.

ENEMIES

Since this species is so well protected, it is largely free from attacks by insects. In early morning, the writer has often seen flocks of sparrows feeding on the ground near the pools, but never did they attempt to feed on the larvae which were so numerous in the mud and shallow water. Herring gulls and kingfishers were seen several times flying over this region from the lake, and the latter often stopped somewhere near the pools, but never has the writer been able to see them feeding on the immature stages of the fly. Domestic fowls, on the other hand, are enemies of this species. Throughout the season fowls' footprints were often found on the mud in the overflowed areas, and several times the fowls while hunting for food were seen to pick up larvae or pupae. Among insects, the only enemy observed was one of the common water striders, *Gerris marginatus*. Once a fly was noticed turned upside down on the water surface; before it regained its natural position it was caught by a water strider. The strider carried the fly around on the surface for about a quarter of an hour, but finally it disappeared in the grasses along the shore.

Not long afterward it came out again with the prey still in its possession. There may be more enemies among the insects, but no others were observed. The writer once found a water mite, Limnochares, attached to the cheek of an adult fly, as an external parasite.

DISPERSAL

Ephydra subopaca may be dispersed, perhaps for a long distance, during the pupal stage. As already mentioned, it is impossible for the adult to make a long journey on the wing. Since the larva, although able to crawl in soft mud, has no means of locomotion elsewhere after the moisture in the mud is all gone, there is no chance for it to travel from one place to another. As soon as the prepupal period is at hand, the perching habit enables the animal to secure stable foothold. Then there comes the possibility of migration, because wherever the supporting object is shifted, the pupa will go with it. Dispersal is facilitated by three characteristics of the pupal stage — one held in common by all insects, and two particularly pertaining to this species: first, during the pupal stage, the animal does not require food; second, the pupa always has a very firm hold on its support, so that there is no danger of its being shaken off; third, the thick and hard puparium enables the animal to stay outside of water for some time, and also serves, as already mentioned, for protection from injury during its journey.

Many times the writer, in lifting a fragment of wood from the pools, found hundreds of pupae, both mature and young, scatterd along the edges of the stick. These could never be removed by shaking or jerking. Several times an enormous number of pupae were found firmly attached to a piece of cord which had been thrown into a shallow pool. Whether in water or in the soft mud area, or exposed to the air, these pupae are able to attain maturity if no extremely unfavorable conditions occur. Attached to such supports, they may be brought from one place to another by train or other carrier, and thus dispersal of the pupae may be accomplished.

Aldrich (1912) lists the localities where this species has been found as follows: Massachusetts, Woods Hole (Melander); Connecticut (Loew); New York, Ithaca, at salt pools (Johannsen); New Jersey, several localities (Smith catalog); Illinois, Gallatin County, at salt pools (Packard); Utah, Box Elder Lake, in salt water, Garfield in brackish seepage, Promontary Point in brackish spring; Idaho, Market Lake, in overflow from

irrigating ditch; Nevada, Hazen, in overflow from irrigating ditch; Winnemucca Lake, in alkaline environment; Walker Lake, in alkaline environment; California, Mono Lake, in near-by seepage; Washington, Soap Lake, Grand Coulee, in alkaline environment.

Aldrich states that the density of the water (salt or alkaline) in which this particular species lives is subject to great fluctuations.

From the experiments described herein, proving that larvae of *Ephydra subopaca* can live in salt solutions of different strengths, varying from 1 to 9 per cent, it follows that there is an ample chance for this species to survive in pools or lakes the salinity of which falls within such limits.

SEASONAL APPEARANCE AND METEOROLOGIC CONDITIONS

To temperature and humidity is largely due the seasonal appearance of this species. Warm weather in late spring causes the adults to appear early, and high humidity in summer causes all stages to appear in great numbers throughout the season. The weather records of the two seasons 1916 and 1917 are different in this respect. In the year 1916 the species appeared much earlier than in the year following, while in 1917 there was a greater abundance of both the adult and the immature stages than in the year before. These differences were due mainly to the temperature and the rainfall in the spring and summer of the two years.

According to the report of the United States Weather Bureau at Ithaca, New York, the average temperature for May, 1916, was 57.6° F., while that for 1917 was 48.4°. The work of the writer began in June, 1916. Although the first appearance in the preceding month was unfortunately lacking in the field record, the field observations convinced the writer that they must have appeared three or four weeks before the work started. During June, adults were found in the salt pools and even in the one the water of which had almost lost its briny character; and the mass of the flies that every day assembled over the water surface did not seem to indicate that they were the ones that appeared first in the season. The writer was informed by Dr. O. A. Johannsen that he had caught many adults in May. The first appearance of the adults is usually in the latter part of this month. In 1917, on the other hand, the appearance was evidently delayed on account of low temperature. Beginning on May 1, the writer frequently visited the pools, looking for adults, but none were found until June 21, when they appeared in large numbers. In June,

1916, larvae and pupae were found in almost every pool, because the adults started to breed early, while in 1917, in the first twenty days, only one or two were found. For such contrast the difference in temperature is considered the most probable cause.

As far as the number in all stages is concerned, the summer of 1917 outstripped the preceding year, in spite of the delay in appearance of the adults. After the adults had appeared, they soon started to breed. High humidity facilitated the hatching of the eggs and the development of the larval and pupal stages, thus bringing forth great numbers of adults. The immature stages were produced in corresponding abundance. There is every reason to believe that the great number of this species found in the summer of 1917 was due to the frequent rains that were so characteristic of that season in this locality. During the previous year the amount of rainfall was considerably less, and this species was correspondingly more scarce.

COMMUNAL LIFE

Being able to live in great fluctuation of density and salinity, *Ephydra subopaca* has a decided advantage over other insects in the salt pools. Here competition or the struggle for existence between this species and all others is by no means keen. Besides *Ephydra subopaca*, the permanent members of the same community consist of five insects, four of which are coinhabitants, while the other is more or less an intruder and an enemy to the adult flies of the species. This latter is the common water strider, *Gerris marginatus*, mentioned in the preceding pages. This insect is, however, very rare. Among the other four the most abundant and common form is the larva of a mosquito, *Aedes curriei* Coq. This larva is numerous in some pools and sometimes it outnumbers the species of Ephydra, but it is not able to endure high salinity. Consequently, the larvae have never been found in pools D, E, I, and II, the salinity and density of which are high (page 365).

Rat-tailed maggots are found in most of the pools. They are able to endure a salinity as high as that of pool D, and in this respect they can compete with the larvae of Ephydra; but the number is far inferior, and only now and then one or two are found, so there never could be very much competition for food and shelter between the two species. A few larvae of Culicoides and a great number of Chironomus are also found

in the water of comparatively low salinity, and the writer has occasionally found a few water mites in such water. But with an overwhelming number and an elastic adaptability to various conditions in pools, Ephydra has so far outstripped its coinhabitants in competition that the principal place in this kind of habitat must be assigned to this species.

HIBERNATION

The larvae which do not pupate in late autumn live through the winter. They usually stay at the bottom of the pools and very seldom are found suspended between the surface and the bottom, as in summer. They are motionless and are covered with mud through the accumulation of sediment. It is hard to distinguish them by looking over the surface of the pools; but in the overflowed areas, where the water is hardly more than three inches deep, a large number of them may be found lying on the muddy bottom. Sometimes, when the heat of bright winter sunshine raises the temperature, a few larvae may be seen crawling slowly. They will not pupate in cold weather but will wait until spring.

The pupae of late autumn will remain undeveloped through the winter. Late in the season large numbers of pupae may be found. In the early spring of the next year pupae are always found before any other stage appears. From these emerge the first adults of the coming season.

Adults are rarely found in winter. On a warm and sunshiny morning one or two may appear, feebly drifting around on water. It is believed that they hide themselves in crevices in the gravelly bank and in the loose soil around the pools in order to winter over.

Hibernation in the egg stage, if it occurs at all, must be very exceptional. According to observations made in the laboratory, the females do not oviposit late in the season, even though the room temperature may be comparatively high. Eggs laid in the early fall remained undeveloped for a long period, and some of them died before winter commenced. Thus there is evidently very little chance for them to hibernate in this stage.

SUMMARY

1. *Ephydra subopaca* has a salt habitat. It is found in the salt pools at Ithaca, the density of which ranges from 1.5 to 7+ in August and from 4 to 11 in September, and the salinity of which varies from 1.76 to

9.7 per cent in August. The salt pools contain several algae and several protozoa, together with some animal pollution.

2. The growth of the larva is largely influenced by temperature and the presence of salt in water.

3. The larva moves by crawling, wriggling, floating, and dropping. Its respiration is at the surface. Its food consists of algae with few protozoa. It prefers to live in stagnant and shallow water, with the amount of salt ranging between 1 and 8 per cent and a solution of from 4- to 5- per-cent salt in the optimum.

4. The larva can live in a limited area of air. It can endure the variation of temperature from 0° to 40° C. It can survive drought for five days.

5. It is significant with the larva that its specific gravity is less than unity.

6. Any mechancial injury which breaks the hypodermis proves fatal to the larva.

7. Pupation is characterized by the perching habit. The pupal period lasts from two to eleven days in the laboratory and from four to five months in the field. High temperature in addition to desiccation is very detrimental.

8. The food of the adult is the same as that of the larva. The adult prefers to stay on the surface of still water. Excessive heat is very detrimental, but excessive rainfall is beneficial. Only heavy frost has a killing effect upon the newly emerged adult. The adults disappear entirely in winter when snow covers the ground.

9. The egg is elongated oval with a reticulated surface. Hatching takes place in fresh water as well as in salt water. The development of the egg is affected by temperature.

10. The habit, the adaptation, the coloration, and the body structure of all stages are protective. Domestic fowls and water striders were the only enemies observed.

11. The dispersal of this species takes place during the pupal stage and is probably achieved by artificial transportation.

12. The flies appear in May or June. High temperature and high humidity in late spring make for an early appearance. Frequent rains favor abundance of them throughout the summer and autumn seasons.

13. This species winters usually in the larval and pupal stages, although a few adults may live through the winter in hibernation.

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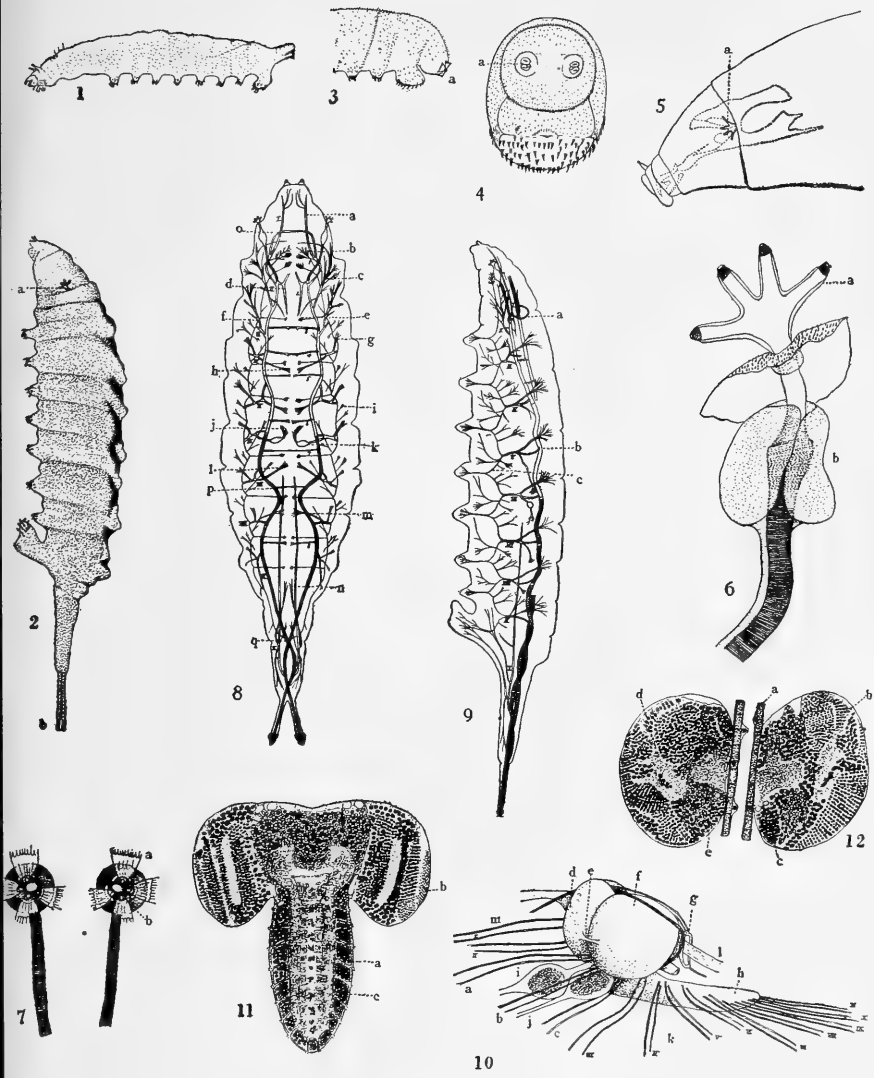
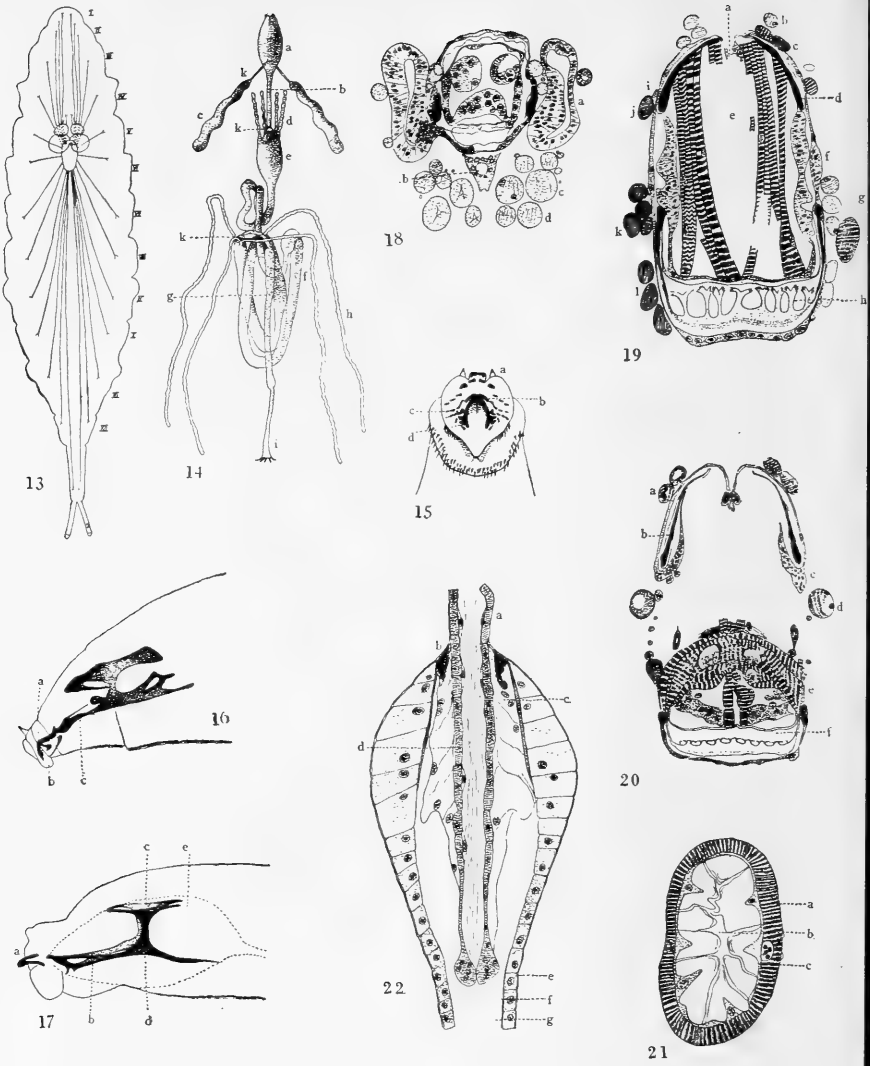


EPHYDRA SUBOPACA

1, First-instar larva; 2, full-grown larva (a, prothoracic stigma; b, posterior spiracle); 3, lateral view of caudal part of first-instar larva; 4, caudal view of same (a, posterior spiracle); 5, relative positions of prothoracic stigma and cephalopharyngeal skeleton (a, prothoracic stigma); 6, enlarged view of stigma (a, stigma; b, imaginal disk); 7, posterior spiracles (a, chitinous membrane; b, spiracle); 8, dorsal view of tracheal system (I-X, outer branches; 1-8, inner branches; a, tracheal branch to muscles of cephalopharyngeal skeleton; b, same; c, tracheal branch to imaginal disk; d, to ring; e, to salivary gland; f, to imaginal disk; g, to dorsal body wall; h, to proventriculus; i, to lateral body wall; j, to mid-intestine; k, to tracheal body; l, to mid-intestine; m, to mid-intestine; n, to hind intestine; o, p, q, commissures); 9, lateral view (a, commissure; b, dorsal trunk; c, ventral trunk); 10, lateral view of nervous ganglion of larva (I-XI, segmental nerves; a, b, c, nerves arising from bases of stalks of prothoracic and ventral mesothoracic imaginal disk; d, optic imaginal disk; e, optic stalk; f, cerebral lobe; g, ring; h, subesophageal ganglion; i, prothoracic imaginal disk; j, ventral mesothoracic disk; k, esophagus; l, dorsal aorta; m, trachea); 11, horizontal section of brain (a, root of nerve; b, retina; c, stroma); 12, horizontal section of cerebral lobes (a, esophagus; b, retina; c, corpus fungiforme; d, trabecula; e, stroma)



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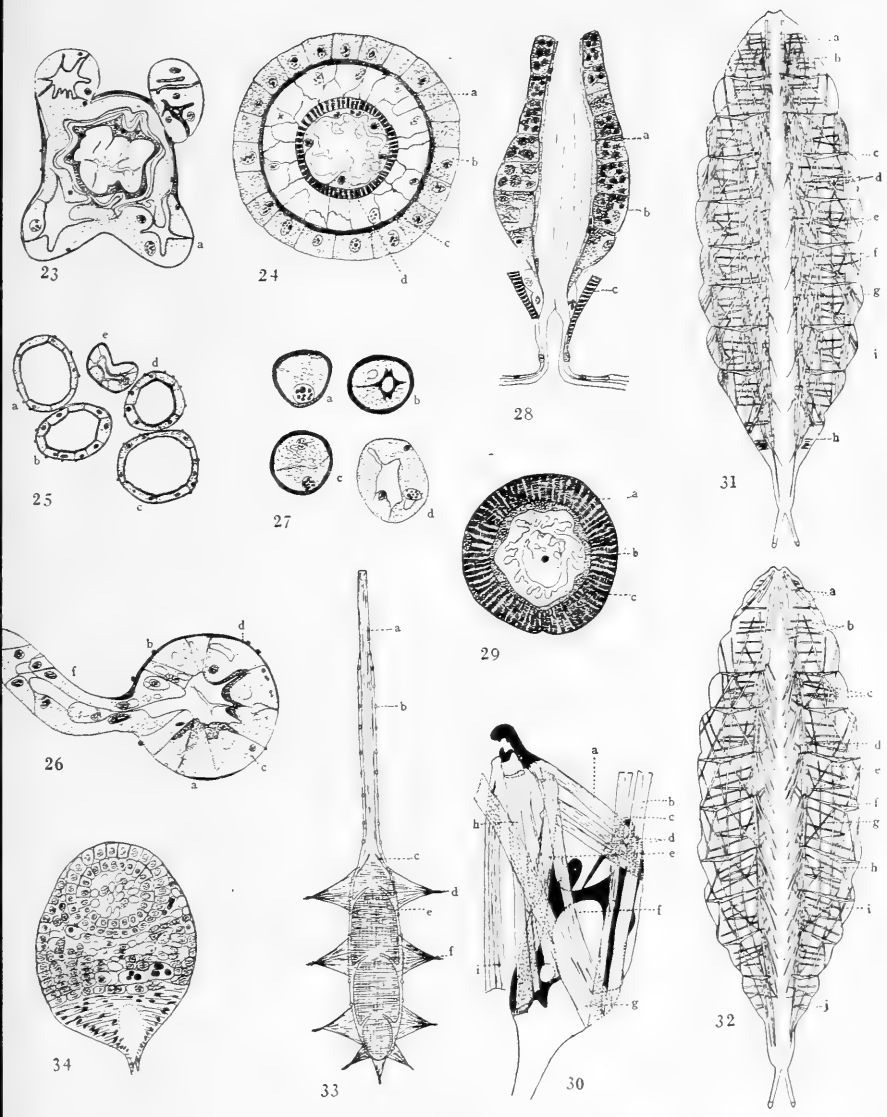
13, Dorsal view of distribution of segmental nerves (I-XII, segments); 14, alimentary system (a, pharynx; b, esophagus; c, salivary gland; d, caeca; e, proventriculus; f, mid-intestine; g, hind intestine; h, malpighian tube; i, rectum; k, imaginal disks); 15, ventral view of oral cavity and second body segment (a, antenna; b, mandibular sclerite; c, tubercles; d, hypostomal sclerite); 16, lateral view of head region of grown larva, showing cephalopharyngeal skeleton (a, mandibular sclerite; b, dental sclerite; c, hypostomal sclerite); 17, lateral view of young larva (a, mandibular sclerite; b, hypostomal sclerite; c, dorsal pharyngeal sclerite; d, lateral pharyngeal sclerite; e, pharyngeal mass); 18, cross section of anterior pharyngeal region (a, imaginal disk; b, common duct of salivary glands; c, cephalic retractor muscle; d, ventral longitudinal muscle); 19, middle pharyngeal region (a, accommodating membrane; d, dorsal longitudinal muscle; c, cephalic retractor; d, pharyngeal sclerite; e, pharyngeal sinus; f, imaginal disk; g, pharyngeal muscle; h, Y-shaped ridges; i, pharyngeal depressor; j, dorsal cephalic protractor; k, stomal dilator; l, mandibular depressor); 20, caudal pharyngeal region (a, cephalic retractor; b, lateral pharyngeal sclerite; c, imaginal disk; d, stomal dilator; e, semicircular dorsal pharyngeal muscle; f, pharyngeal cavity); 21, cross section of esophagus (a, circular muscle; b, lumen; c, epithelium); 22, longitudinal section of esophageal valve (a, esophagus; b, imaginal cells; c, blood space; d, sphincter; e, epithelium, or ventriculus; f, basement membrane; g, lumen of ventriculus)



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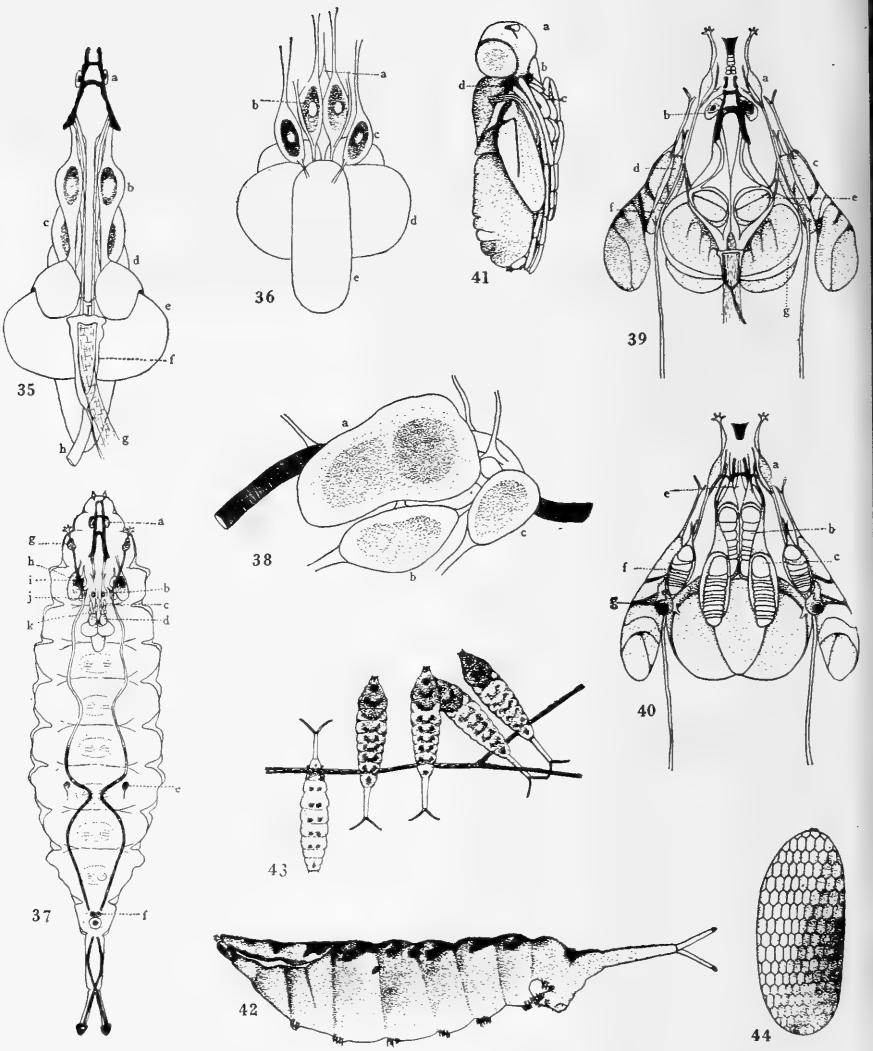
23, Cross section, showing insertion of caeca (a, caecal tube); 24, cross section of proventriculus (a, striated border; b, epithelium; c, blood space; d, circular muscle of sphincter); 25, cross section through convoluted alimentary canal (a, b, c, d, mid-intestine; e, hind intestine); 26, cross section, showing insertion of malpighian tube (a, circular muscle; b, longitudinal muscle; c, epithelium; d, basement membrane; f, malpighian tube); 27, cross section of malpighian tubes (a, b, c, tubes; d, common root of two tubes); 28, longitudinal section of rectum (a, epithelium; b, muscular wall; c, muscle); 29, cross section of rectum (a, circular muscle; b, epithelium; c, intima); 30, muscles of cephalopharyngeal sclerites (a, mandibular extensor; b, pharyngeal depressor; c, dorsal cephalic protractor; d, e, f, stomal dilators; g, ventral cephalic protractor; h, mandibular depressor; i, ventral cephalic retractor); 31, muscles of dorsal body wall (a, dorsal cephalic retractor; b, demi-annular; c, lateral intersegmental; d, external dorsolateral oblique; e, internal dorsolateral oblique; f, lateral longitudinal; g, dorsal longitudinal; h, anal; i, lateral); 32, ventral body wall, with muscles (a, dorsal cephalic retractor; b, ventral cephalic retractor; c, internal ventral oblique; d, external ventral oblique; e, lateral longitudinal; f, intersegmental; g, internal ventro-lateral oblique; h, external ventro-lateral oblique; i, ventral longitudinal; j, anal); 33, dorsal view of vascular system (a, dorsal aorta; b, pericardial body; c, valve; d, alar muscle; e, f, ostia); 34, longitudinal section of gonad



EPHYDRA SUBOPACA]

35, Dorsal view of imaginal disks (a, proboscis, b, antennal and frontal; c, prothoracic leg; d, mesothoracic leg; e, cerebral lobe; f, ring; g, dorsal aorta; h, esophagus); 36, ventral view (a, median string; b, prothoracic leg; c, mesothoracic leg; d, cerebral lobe; e, subesophageal ganglion); 37, general arrangement of imaginal disks (a, proboscis; b, antennal and pronotal; c, prothoracic leg; d, optic; g, dorsal prothoracic; h, wing; i, metathoracic; j, haltere; k, mesothoracic; f, anal; e, gonad); 38, external view of posterior thoracic imaginal left side (a, wing; b, metathoracic; c, haltere); 39, dorsal view of imaginal disks of prepupal stage (a, dorsal prothoracic; b, proboscis; c, wings; d, metathoracic; e, frontal; f, haltere; g, optic); 40, ventral view (a, dorsal prothoracic; b, prothoracic leg; c, mesothoracic leg; e, median string; f, metathoracic; g, haltere; 41, pupa (a, antenna; b, labral part of proboscis; c, coxa of leg; d, spiracle); 42, puparium; 43, pupae perching on stick; 44, egg

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AGRICULTURAL EXPERIMENT STATION

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ: ITS BIOLOGY, ANATOMY, AND HISTOLOGY

LAURA FLORENCE

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CONTENTS

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THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ: ITS BIOLOGY, ANATOMY, AND HISTOLOGY[1]

LAURA FLORENCE

Because of their habitat on man and beast, lice have been known from the earliest times. Their systematic position has been a subject of controversy for more than a century, and the hog louse, on account of its large size and wide distribution, has frequently been used for the study of the morphology of the order. About the middle of the nineteenth century there was a controversy among physicians and entomologists as to the nature of the mouth parts of the pediculi infesting man, and the mouth parts of the hog louse were brought into the discussion by Burmeister. A detailed account of this discussion is given in a paper by Schjödte (1864, English trans. 1866:213). Since the pediculi infesting man have been shown to be an etiological factor in the transmission of certain diseases, much accurate work has been done on their life history and morphology, and the many points of interest raised through such detailed study suggested that a parallel study of an animal parasite might be equally profitable. The aim of the present work has been to give an accurate account of the general internal anatomy of the hog louse, with a detailed description of the histology of certain parts. The relation between the parasite and its host has not been considered, and references to veterinary literature do not appear in the bibliography.

The study was begun in 1917 in the Entomological Laboratory of Cornell University under Dr. William A. Riley, now of the University of Minnesota, and was continued under Dr. O. A. Johannsen, to both of whom thanks are due for helpful criticism. Since June, 1918, by the courtesy of the Scientific Directors of the Rockefeller Institute, and, in particular, of Dr. Theobald Smith, Director of the Department of Animal Pathology, it has been made possible for the writer to complete the investigation.

[1] From the Department of Entomology of the New York State College of Agriculture at Cornell University, and the Department of Animal Pathology of the Rockefeller Institute for Medical Research. Also presented to the Faculty of the Graduate School of Cornell University, June, 1920, as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

HISTORICAL REVIEW

According to Moufetti (1634, English trans. 1658), the earliest reference to the hog louse is to be found in the works of Albertus, a writer of the twelfth century, who named the insect *Pediculus urius*. Moufetti retained this name and described the louse as somewhat larger than that infesting oxen and calves, and so hard that it could not be crushed between the fingers. Linnaeus (1758:2915) described the louse under the name *Pediculus suis*. Panzer (quoted by Stevenson, 1905), in 1798, followed the nomenclature of Linnaeus and stated that in the classification of Fabricius this parasite was placed "with *Pediculus asini* of Redi (1671)." Leach (1817:65) broke up the genus Pediculus into four genera, Phthirus, Haematopinus, Pediculus, and Nirmus, making the hog louse the type of the new genus Haematopinus. This classification was not immediately accepted, and Nitzsch (1818:305) revived the old name of Albertus. He was followed in this by Burmeister (1839:58), who gave the synonymy and a brief description of the louse, and later (1847:569) gave a detailed description of the structure of the mouth parts.

Systematic descriptions and figures of the species are to be found in the monographs of Denny (1842:34), Giebel (1874:45), and Piaget (1880: 654), of which the last is the most detailed. More recent and popular descriptions are given in three bulletins of the United States Department of Agriculture. Two of these are the work of Osborn (1891 and 1896), and in them the sections on the hog louse are identical. He calls attention to "a curious provision in the feet for strengthening the hold upon the hair, which does not seem to have been hitherto described." The third bulletin, written by Stevenson (1905), is valuable on account of the complete synonymy and the extent of the bibliography.

Between 1903 and 1906 a number of papers relating to the systematic position of the Pediculidae appeared in Europe. Most authors confined their investigations to the mouth parts, and for a time a bitter controversy was waged between Cholodkovsky of St. Petersburg and Enderlein of Berlin. Cholodkovsky (1903:120 and 1904:368) studied numerous sections of the head of the embryo of *Pediculus capitis*, while Enderlein (1904 and 1905), using cleared preparations and gross dissections, studied the hog louse in greatest detail of all the species used. Cholodkovsky's findings in regard to adult lice were confirmed by his pupil, Pawlowsky (1906:156), whose paper contains a discussion and criticism of the literature to date.

In the same year Gross (1903:347) published the results of his investigation of the ovaries of the Mallophaga and the Pediculidae. In his introduction he sums up an earlier investigation as follows:

> Handlirsch (1903) places them [the *Pediculidae*] in a special order Siphunculata, Meinert next the Mallophaga in his subclass Blattaeformia. Börner (1904) gives them the same name, but raises the family to the rank of a suborder which, together with the Corrodentia, the Thysanoptera, and the Rhynchota, forms his order of Acercaria. Cholodkovsky (1904) joins the Pediculidae and the Mallophaga in one order, related with the Orthoptera rather than with the Hemiptera, for which he proposes the name Pseudorhynchota. Finally, Enderlein (1904) interprets the Pediculidae as one with the Anoplura — a name originating with Leach — an order lying near to the Rhynchota. None of the four opinions mentioned is to be considered as entirely new. They are all found in similar form in the old entomologies of the preceding century.[2]

Gross next emphasizes the importance of using other less delicate organs than the mouth parts as a basis for comparison.

A historical review of lice from the time of Aristotle, together with an account of the general characteristics of the order and descriptions of species, was prepared by Von Dalla Torre (1908) for the *Genera Insectorum*. For this Enderlein's work served as a basis, as it did also later for the section on lice in the textbook of Patton and Cragg (1913:525). Neumann (1909:530) criticized Enderlein's splitting-up of the old genus Haematopinus of Leach as being for the present unnecessary, and retained the original classification in his descriptions of species (1911). Mjöberg (1910) published comparative studies of Anoplura and Mallophaga dealing with both the morphological and the systematic aspects of the question. Previous to this time only the dissertation of Ströbelt (1882, English trans. 1883:73) had dealt with the anatomy of a species of Haematopinus — *H. tenuirostris*, now *Linognathus vituli*. The observations of the earliest workers — Hooke (1665), Swammerdam (1682), and Leeuwenhoek (1695) — and the investigations of the scientists of the latter half of the nineteenth century, dealt exclusively with the species infesting man. The presence of great armies in the field during the five years from 1914 to 1918, inclusive, compelled intensive studies of these species from medical and sanitary standpoints, with the subsequent publication of many valuable papers, of which a liberal use has been made in interpreting the anatomy of the species under investigation.

The classification followed throughout this paper is that suggested by Nuttall (1919:329) in a recent review of the systematic literature of the

[2] Translated from the original German.

Pediculidae. He points out that the order Anoplura Leach 1817 contains two suborders — Siphunculata Meinert 1891 and Mallophaga Nitzsch 1818 — and says (page 332 of reference cited): "Since, however, the name Anoplura Leach (1817) was applied to both Siphunculata and Mallophaga, and in this sense agrees with modern views, it should henceforth be used in its original sense only, there being no justification for continuing to apply it to Siphunculata alone."

BIOLOGY

The hog louse is the largest louse affecting domestic animals and is of common occurrence wherever the hog is found. The hog is its only host, and when not molested the parasite is likely to increase in large numbers and cause an unthrifty condition in a herd. The lice frequent the folds of the skin on the neck and the jowl, the inside and the base of the ears, the inside of the legs, the flanks, and, in smaller numbers, the back, where they crawl under the scales to get in contact with the new skin. They are well adapted for experimental work, because they are easy of access and feed readily on man, while their size and their habit of taking hold of any object placed in front of them lessen the difficulty of keeping them in confinement.

From the time of hatching, hog lice feed readily on man if they have not become weakened through too long fasting. During the course of this investigation hundreds of lice have been fed on the forearm without any resulting reaction, except, in a few cases, a slight redness which disappeared within half an hour, and, in cases in which the mouth parts were inserted but no blood was drawn, a slight swelling which disappeared within an hour. This is contrary to the finding of Sikora (1915:536), who saw no reaction on the first or the second day of the feeding but states that thereafter the skin turned red in an area from 1 to 5 millimeters around the point of puncture and swelled slightly, remaining thus for more than twenty-four hours. Recently Moore and Hirschfelder (1919:8) have published a detailed account of serious pathological effects of the bite of the clothes louse and clinical observations of the resulting illness. According to Stevenson (1905:12),

> Stockmen handling hogs often become temporary hosts of the louse, but it has never been known to remain for any length of time on the human body and is not known to exist on any animal other than the hog. Attempts made at this laboratory [United States Bureau of Animal Industry] to propagate *Haematopinus suis* on dogs have met with repeated failure

Several attempts have been made to feed the lice on guinea pigs, but without success. The dense hair of the pigs hampers the movements of the lice, and, if shaving be resorted to, the lice are left without a foothold. If the finger be pricked and lice brought in contact with the freshly escaped blood, the lice immediately move away. Widmann (1915 b: 1337) described a similar reaction in man-infesting lice, which refused to feed on various organs just removed from freshly killed mice.

When placed on the arm, hog lice may feed at once or may move about more or less rapidly. When walking they appear to move sideways as often as straight forward with the head in front. The peculiar structure of the feet, first described by Osborn (1891:20 and 1904:107), enables the lice to grasp the hairs on the arm. The tibia (Plate LVIII, 1) increases at the distal end to twice the width of the proximal end, and the dorsal half only articulates with the tarsus. The remaining part is concave and its ventral border is drawn out to a spur, bearing a stout spine at the apex. In the concavity rests a stalked, protrusible, subcircular pad bearing two spines and two hairs. On the inner edge of the tarsus, in line with the surface of the extended pad, is a blunt process bearing a spine. The inner surface of the claw is slightly serrated. In holding a bristle or a hair, the claw is bent over to rest on the tibial spur and the pad is pushed against the opposite side of the bristle, thus preventing the insect from slipping. Enderlein (1904:141), to whom Osborn's earlier description was evidently unknown, describes the pad as a strongly chitinized skeletal piece of triangular shape. In specimens cleared in potash and mounted under a cover glass it frequently has this shape, while in living and in uncleared specimens it always appears subcircular. Enderlein names this pad the *pretarsal sclerite*, which name is retained by Neumann (1911: 407) in his description of the insect.

The earliest description of a louse feeding is that of Hooke (1665:211-213). He described the passage of blood from his arm into a louse which he had placed there after it had fasted for several days, and the working of a pumplike apparatus in the head. Swammerdam (1682, English trans. 1758:33-35) gave a more detailed description, but he disagreed with Hooke's description of the mouth parts, saying: "The louse has neither beak, teeth, nor any kind of mouth, as Dr. Hooke described it, for the entrance into the gullet is absolutely closed; in the place of all these, it has a proboscis or trunk, or, as it may be otherwise called, a pointed and

hollow aculeus or sucker, with which it pierces the skin, and sucks the human blood." He also described the pumplike structure in the head, the peristalsis of the alimentary tract, and the ejection of feces during feeding. Leeuwenhoek (1695) described the hook-bearing part of the proboscis and its eversion during feeding, in addition to other characteristic actions associated with the process.

When fed in captivity, the louse moves its head back and forth close to the surface of the arm and rapidly jerks the antennae up and down. Then, with the head held at right angles to the body, it seems to anchor itself to the skin, probably by the everted teeth of the haustellum. While the stylets are being inserted, the thorax and the abdomen are raised and gently rocked from side to side, and the claws make irregular scratching motions. After the insertion the insect is holding itself in a more or less straight line and at an angle of from 40° to 45° with the arm. As the feeding progresses the body is gradually lowered, until it rests on the arm and with its head forms an oblique angle The act of sucking blood can best be watched in freshly molted specimens. The blood is first seen anterior to the eyes in the pumping pharynx, which dilates and contracts with great rapidity, driving its contents into the true pharynx (larynx of Enderlein), whence they disappear under the brain to reappear as a thin red line in the slender esophagus before this passes under the fat cells and muscle of the thorax. Throughout the process a continuous peristalsis passes along the whole alimentary tract, but this has manifestly no connection with the drawing of the blood, as suggested by Widmann (1915 a: 290). It seems rather to be a means of removing from the posterior region of the stomach and from the intestine the débris of the preceding meal, since it is the habit of the hog louse — at any rate when kept and reared in captivity — to continue feeding until not only all the feces, but also a drop of blood, have been ejected. The latter may be pushed out by the interlocking of the six longitudinal folds of the epithelial lining of the intestine immediately behind the stomach, in order to prevent the escape of the blood from the mesenteron during digestion. At the first feeding after hatching, no blood has been seen to be ejected, and in some cases after the second feeding feces but no blood have been ejected. The average length of a meal is from eight to twelve minutes, but sometimes it lasts from twenty to thirty minutes, and at the close the mouth parts are apparently withdrawn by a short jerk of the head. Occasionally lice

have gorged themselves and have been seen to turn pink within a few minutes, owing to the rupture of the stomach and the spread of blood through the colon. This phenomenon, which has been invariably followed by death, has been seen also by Nuttall (1917 d:173) in the pediculi infesting man. The unfed louse is of a grayish color and much wrinkled, while the fed louse has a highly refractive, smooth tegument showing very clearly the areas of stronger chitinization. During keeping and rearing, immature lice have been given four, and adult lice three, opportunities for feeding in twenty-four hours, and these were not always taken advantage of. Temperature influences the rate of digestion, and the higher the temperature in which lice are kept, the more frequent must be the opportunities given them for feeding.

Sexual maturity is attained on the third day after the final molt, when, with or without fecundation, egg-laying begins. The position for copulation has been observed a number of times. While a female was feeding and still had the abdomen somewhat elevated, the male crawled underneath and interlocked his first and second pairs of legs with the second and third pairs of the female. She at once raised her abdomen, resting only on the head and the first pair of legs and bearing the whole weight of the male. The abdomens of both were curved dorsad and the male was seen to insert the parameres (dilator of Nuttall) into the sexual orifice of the female. Gradually the bodies were lowered until the third pair of legs of the male rested on the arm, and the head was under that of the female. They remained in this position for almost ten minutes, during which time the male constantly stroked the head of the female with his antennae. In its main features this resembles copulation in the pediculi infesting man as described by several workers, the most detailed account being that of Nuttall (1917 a:316). Hog lice in captivity have not been seen to remain in copulation longer than from ten to fifteen minutes, while the species infesting man crawl into hiding and remain so for several hours.

The eggs (Plate LVIII, 2) are laid, one at a time, on the bristles of the hog and are attached to them by a clear cement. They are most abundant on the lower parts of the body. The egg-laying process has been watched on the human arm during feeding. After drawing blood for almost ten minutes, the female withdrew the mouth parts but remained stationary, holding the end of the abdomen bent downward in an unusual manner.

Neither feces nor blood was ejected from the anus, but a drop of hyaline fluid escaped from the sexual orifice almost simultaneously with the pointed end of an egg. After a few seconds the louse moved away, leaving the egg attached to a hair on the arm. The position of the gonopods could not be seen, but the posterior lobes of the ninth abdominal segment surrounded the hair on which the egg was laid. According to Sikora (1915:536), who has described the act of egg-laying on a bristle by a hog louse in captivity in a vial, the insect remained motionless for almost ten minutes after the first appearance of the egg, and then moved off leaving the egg attached to the bristle. Watts (1918:9) says, "The entire operation requires but a few seconds, so that one seldom sees a female lay an egg unless watching closely for some time." In the ovaries the eggs are oriented according to Hallez' law, and, when laid, the ventral surface is attached to the bristle. The cement surrounds the bristle but does not appear to surround the egg, which is attached to the bristle between its transverse median line and its posterior end. One or more eggs may be laid on the same bristle, not always pointing in the same direction. After attachment we have always found them immovable, but Watts (1918:9) states that he has found they can be slipped along the hairs and are often pulled away from the body by the rubbing of the animal. This, however, does not agree with his earlier statement on the same page, that "each egg is glued to the base of a hair and is laid so that the smaller end practically touches the skin of the host, which keeps the egg warm until it hatches, several days later"; and, since the diameter of the bristle diminishes toward the tip, the cement ring large enough to surround the base of the bristle would tend to slip off, carrying the egg with it, thus causing an excessive mortality not provided for by overproduction.

In captivity the eggs are laid on bristles or threads of gauze, and the number laid daily appears to depend on the opportunity to feed, as the following table shows:

Opportunities of feeding in 24 hours	Number of eggs laid in 24 hours	Authority
Four	2	Sikora
Continuous	4	Sikora
Continuous for 7 days	3	Claassen[3]
Two	1–2	Florence

[3] Unpublished data kindly communicated to the writer by Professor P. W. Claassen, of the Department of Entomology, Cornell University.

The last data relate to a female reared in captivity. Three days after the last molt, when put on the arm to feed, she moved rapidly about for thirty minutes, repeatedly elevating the posterior end of the abdomen, and made no attempt to draw blood. She was returned to the vial and two hours later was given another opportunity to feed, when an egg was found attached to a bristle in the vial. Twice a male was placed in the vial for some hours, but in neither case was copulation seen to occur. During a period of sixteen days eighteen eggs were laid, none of which hatched. The female died six days after laying the eighteenth egg, and gross dissection showed the ovaries very much shrunken. That oviposition continues without fecundation has been observed by various workers, and the unfertilized eggs are easily recognizable because they quickly change color and shrivel up.

When laid, the egg is an iridescent pearly white. As development progresses it becomes more opaque, and toward the end of the incubation period it appears light amber in color. Its average length is 1.5 to 1.75 millimeters, and its average breadth at the widest part is 0.5 to 0.75 millimeter. It is symmetrical, tapers posteriorly, and is bluntly rounded at the anterior end, where the operculum is situated. The widest part is just behind the operculum (Plate LVIII, 2). The surface is covered with small punctations, which are somewhat larger on the operculum than on the main part of the egg. The junction of the egg with the operculum is indicated by a small ridge bearing striations parallel to the longitudinal axis of the egg.

Hatching has not been observed, but eggs have been seen shortly after being hatched. The operculum opened away from the bristle and remained attached to the egg by a small hinge; protruding from the egg was a small fragment of the vitelline membrane (Plate LVIII, 2). A number of authors have mentioned points in connection with the hatching of pediculi infesting man, and Sikora (1915:530) was the first to give a short description of the process, which has since been confirmed and extended by Nuttall (1917 d:148). Probably in the hog louse the process is essentially the same. The following data show that the period of incubation is influenced by temperature, and suggest a reason for the seasonal variation in the development of the eggs on the hog:

Conditions	Eggs hatched after	Authority
On hog	About 5 days	Coburn[4]

[4] Data from Coburn (1888).

Conditions	Eggs hatched after	Authority
On hog	From 13th to 20th day, maximum about 16th day	Watts
Room of ordinary humidity, at temperature of 85° F., in September	From 15 to 16 days	Stevenson
Same conditions, but eggs kept in a closed dish containing a receptacle filled with water	12 days	Stevenson
Temperature by day of 26° C. and by night of 35° C.	17 days	Sikora
Incubator at constant temperature of 37° C., dry heat	11 to 12 days (5 eggs hatched, out of 24)	Florence
In vials, worn constantly next the body	14 days (9 eggs hatched, out of 19)	Florence
Conditions as in last preceding	13 days (4 eggs hatched, out of 5)	Florence

The period of incubation evidently lies between twelve and twenty days, with a minimum period of about thirteen to fourteen days when the eggs are kept constantly at body temperature. It is interesting to compare this with the recent work of Bacot and Linzell (1919:388), who found the incubation period of the eggs of the horse louse, *Haematopinus asini*, to be apparently from sixteen to twenty days, and the minimum period under natural conditions about fifteen to sixteen days.

In the course of their development hog lice undergo three molts, and rearing in captivity has proved the cycle from egg to egg to occupy from twenty-nine to thirty-three days. The life history, as we have observed it, is summarized in the following table:

Time from laying to hatching of eggs	13 to 15 days
First molt occurred after	5 to 6 days
Second molt occurred after	4 days
Third molt occurred after	4 to 5 days
Sexual maturity occurred after	3 days

Time of development from first-stage larva to mature adult	16 to 18 days
Temperature and other conditions	35° C., continually next to body, in vials
Number of feedings in 24 hours	1 to 4
Duration of cycle from egg to egg	29 to 33 days

THE EARLY STAGES

The newly hatched louse has 5-segmented antennae and a 9-segmented abdomen, as are found in the adult. The claws and the pad, already described, are present as in the adult, but no joint between the tibia and the tarsus appears until after the final molt (Plate LVIII, 1 and 5). Attention was drawn to this point by Gillette in his brief description of the species written for Coburn (1912:497). The head is large in proportion to the almost colorless body. Only the claws, and the sides of the head in the region of the clypeus, show marked chitinization. During the first instar (Plate LVIII, 3) the dark color gradually extends along the lateral and posterior dorsal regions of the head and the thorax, the legs become more strongly chitinized, and there is some indication of the transverse abdominal plates. The chitinous plates of the pleurites are represented by small, light brown spots close to the spiracles. In the second instar (Plate LVIII, 4) the chitinization is generally more marked, but the buccal tube can still be clearly seen through the integument. The transverse abdominal plates are more developed, the plates of the pleurites are approximately four times as large as in the first instar, and between these two are small circular chitinous areas. In the third instar (Plate LVIII, 5) the head is more strongly chitinized and the buccal tube can no longer be seen throughout its length. The plates of the pleurites resemble those of the adult but are somewhat lighter in colour. The ninth abdominal segment shows no chitinization but is turned slightly dorsad, and the first antennal segment, which in the previous stages was almost of the same diameter as the four other segments, is now considerably larger than these. At the third molt the chitinous plates, which are the external indications of sex, appear at the posterior end of the body. In both male and female, maturity is indicated by a sternal chitinous plate which appears on the thorax about the third day after the final molt (Plate LVIII, 6). The

mature female averages about 4.6 millimeters long by 2.19 millimeters at the broadest part of the abdomen, and the male averages about 3.9 millimeters long by 2.1 millimeters broad. The following table gives the average measurements throughout the life history:

Age	Instar	Number of feedings since preceding molt	Length (millimeters)	Breadth (millimeters)
Newly hatched	1	0	1.00	0.50
12 hours	1	3	1.25	0.50
7 days	2	(?)	1.75	0.75
$8\frac{1}{2}$ days	2	8	2.25	1.00
$9\frac{3}{4}$ days	3	1	2.50	1.00
$10\frac{1}{2}$ days	3	3	2.75	1.25
14 days	4	1	3.00	1.25
$15\frac{3}{4}$ days	4	4	3.25	1.50
18 days	4	2	4.00	2.00
Mature female	.....	.....	4.60	2.19
Mature male	.....	.....	3.90	2.10

In immature lice the lines along which the tegument ruptures at molting are very distinct. When about to molt the insect raises itself until only the posterior end of the abdomen, and the claws of the second pair of legs, are touching the surface on which it rests, the back has a humped appearance, and the head is bent downward at right angles to the body. The first rupture is along the dorsal median line of the thorax and gradually extends caudad to the fifth or sixth abdominal segment and cephalad to the frons, where it divides, passing to the base of each eye. Air is sucked up into the pharynx and passes through the alimentary canal to escape at the anus. The body is inflated, pushed through the dorsal ruptures, and so drawn away from the old skin. The body is lowered until it touches the hair or bristle on which the louse is resting, when the legs are folded laterally across it and the ventral surface of the thorax and the abdomen (Plate LVIII, 7). The head and the thorax are gradually drawn upward until the eyes and the proximal segments of the antennae are seen, disclosing at the same time on the old skin a ventral T-shaped rupture, the stem of the T lying along the median line from a point midway between the bases of the antennae to the prosternum, where there is a

transverse split; the chitin on each side of the median rupture is stretched back so that the opening resembles a triangle. The first pair of legs is next withdrawn, and these, pushing down the skin, help in the final freeing of the head and the mouth parts. These now occupy their normal position, and the second and then the third pair of legs are withdrawn, pushing the insect forward and freeing it from the old skin, which remains anchored to the surface upon which the insect has emerged. The process took place when a louse had been put on the arm to feed and was watched through a binocular. From the first rupture of the old skin until the complete emergence of the insect, thirty minutes elapsed; Sikora (1915: 525-526) describes the process in *Pediculus vestimenti* as lasting but five minutes. No description of the act has been found in the literature of the hog louse, and the slowness in the case observed may have been due to the unnatural environment of the insect; moreover, death followed within an hour of molting.

THE ADULT LICE

The male and the female are recognized by their difference in size, the shape of the abdomen, and the structure of the two posterior abdominal segments. Both are without pigmented eyes, but the projections on the sides of the head have a lateral, slightly convex, refractive surface suggestive of a lens. While the thorax of the female is somewhat shorter and broader than that of the male, the legs of the sexes are identical, showing no modifications for clasping in relation to copulation. No constant variations in pigmentation have been observed.

THE MALE

The abdomen of the male is considerably shorter than that of the female, so that, although it measures the same or even slightly less in its widest region, it appears considerably broader. The tergites of segments 1 and 2 are small, but clearly defined. Hairs are present in each abdominal segment in a transverse row. Posteriorly the abdomen is rounded; the terminal segment curves dorsad and anterior, bringing the rectal and sexual orifices into a dorsal position (Plate LVIII, 8). On the ventral surface there is a strongly chitinized plate of characteristic shape extending from the transverse median line of segment 7 through segment 8 to segment 9, its posterior edge being visible from the dorsal aspect of the

abdomen. Anterior to this plate, in segments 7 and 6, the anterior end of the basal plate can be seen shining through the integument (Plate LVIII, 9).

THE FEMALE

In the female, as already said, the abdomen is longer than in the male, and in consequence it appears more slender. The tergites of segments 1 and 2 are similar to those of the male. Hairs are fewer in number and arranged with much less regularity. The ninth segment has a deep indentation on the posterior median line, and the lateral regions are modified into rather blunt, strongly chitinized processes pointing inward and slightly ventrad, apparently a modification for clasping the bristle during egg-laying, and, according to Mjöberg (1910:216), not unusual in Siphunculata (Anoplura). On the dorsal surface of the segment there is a strongly chitinized plate extending onto each projection, and between it and the edges of the indentation is a row of stout hairs (Plate LVIII, 10). On the ventral surface the gonopods lie on segment 8. They present a striking contrast to those of the pediculi infesting man, in that they are quite flat and lie widely apart. They are flat processes, narrowing posteriorly, and their median free border is somewhat strongly chitinized and set with a row of stout hairs. Anteriorly they are joined by a fold of the integument which projects caudad in two blunt points (Plate LVIII, 11). They have arisen, apparently, as an infolding of the integument of the segment, and may be considered homologous with the gonopods of the Trichodectidae as described by Morse (1903:609).

THE INTEGUMENT AND BODY WALL

The integument is tough rather than hard, and chitin is well developed only in certain clearly defined regions. Sculpturing of the cuticula, described by Mjöberg (1910:185) as typical of most Siphunculata (Anoplura), is absent from this species. In the head the cuticula is strongest along the sides, where the muscles controlling the backward movements of the pharynx are inserted, and in two transverse bars — one in the region of the clypeus, where the muscles of the pumping pharynx are inserted, and a second in the frons, where the muscles of the true pharynx are inserted.

Where the head passes into the thorax a ring of chitin forms the neck, and from its median dorsal surface two chitinous processes extend into

the thorax. These were described in this and other Siphunculata (Anoplura) by Enderlein (1904:126), who named them "Hinterhauptvorsatz" and thought that morphologically they probably originated as tendons of the retractor muscles of the head. Mjöberg (1910:202-203) named them the "occipital apodeme." Gross dissection reveals the continuation of these processes as muscle bands having their origin on the apodeme of the metathorax, while muscles controlling the lateral movements of the head are inserted on their posterior lateral borders.

The dorsal surface of the thorax is strongly chitinized and the segments are completely fused with one another. In mature lice the sternal plate is present on the ventral surface. On the prothorax, and also on the anterior angles of the sternal plate, is a pair of very small openings approximately 0.03 millimeter in diameter, which are present at all stages of development (Plate LVIII, 6, 8, and 10) and have been passed over or variously described up to the present time. Stevenson (1905:15), in his description of the thorax, says: "On the ventral surface between the appendages is a chitinous shield. In each anterior lateral angle of this shield or plate is an opening called the osteole, leading from a canal that extends cephalad." Mjöberg does not mention either of the pairs of openings, and Neumann (1911:407) describes "a pair of very small thoracic stigmata"[5] and "a small stigma in each anterior angle"[5] of the sternal plate. Patton and Cragg (1913:548) describe both pairs of openings as stigmata. On the sternal plates of seventeen species of Siphunculata (Anoplura) figured by Kellogg and Ferris (1915: Pl. IV), no such openings are present.

Gross dissection has shown that these openings are quite different from the stigmata of the tracheae, are without a closing device, and communicate with a canal which has no connection with the respiratory system. The dorsal openings on the prothorax are connected with those on the sternal plate by a rigid, uniformly chitinous canal passing directly dorsoventral laterad of the thoracic tracheal trunk. One short branch is given off almost at right angles to the main stem and at about one-third of the total length of the latter from its dorsal surface, and passes caudad terminating in the transverse band of muscle which lies between the second pair of legs (Plate LVIII, 12). Series of cross sections made through the

[5] Translated from the original French.

thorax at various angles after impregnation of the tissue with silver chromate proved conclusively that the structure has no connection with the tracheae and that the canals are unmodified ingrowths of the body wall. They are composed of chitinous cuticula covered with a layer of small hypodermal cells, and form a rigid internal frame, analogous to the skeleton of higher animals, for the partial support of the muscles of the first and second pairs of legs and a transverse muscle of the thorax. No communication between these and a canal extending cephalad, as described by Stevenson, has been found. They are to be regarded as a paired apodeme of the prothorax and the prosternum.

In the region of the metathorax on the median line there is a marked ingrowth of the cuticula, which forms the center of a ridge-like thickening on the inner surface of the segment. This ridge serves for the insertion of the muscles of the neck, the legs, and the dorsal abdominal plate, and may be named the *metathoracic apodeme.* In the abdomen the segmentation is clearer on the dorsal than on the ventral surface. Segments 1 and 2 are small and have the appearance of belonging to the thorax. As already said, these tergites are clearly defined in both sexes. Segments 3 to 8 have strongly chitinized plates on the pleurites and moderate chitinization of the tergites, while the sternites are almost colorless. The primary cuticula is very thin and can be dissected off with ease from the secondary cuticula, which is of a leathery consistency and in sections has a striated appearance as if deposited in layers. When stained with hematoxylin and eosin the secondary cuticula stains pink except in the strongly chitinized regions, where the primary and secondary cuticulae both retain their yellow color.

The hypodermis underlying the cuticula is made up of uniform cells which become longer and more slender on either side of the trichogen cells. The latter are considerably larger than the hypodermal cells and their basal part is subcircular, and in some cases multinuclear sensory cells lie alongside them sending a prolongation into the hair.

THE RESPIRATORY SYSTEM

Hooke (1665) saw numerous tracheae intimately connected with the fat cells of the louse, but did not recognize their true function. Swammerdam (1682, English trans., 1758:32) saw seven pairs of stigmata with their tracheae. He described their structure and their numerous branches

passing among the viscera, pointing out the resemblance between them and the windpipe of man. Landois (1864:12, 1865 a:45, 1865 b:499) gave the first complete descriptions of the general respiratory system, describing in detail and figuring the closing apparatus of the tracheae of Phthirius. Then followed Ströbelt's (1882:106) description of *Linognathus vituli* (*Haematopinus tenuirostris*). Both writers agreed in the general arrangement of the tracheae and the number of stigmata, but considered those of the abdomen as being situated on segments 2 to 7, an opinion held earlier by Denny (1842:34) and later by Stevenson (1905:15) and by Neumann (1911:407). Mjöberg (1910:218) described the general system for Siphunculata (Anoplura) and compared it with that of Mallophaga. Harrison (1916a:101) worked on the respiratory system of the Mallophaga, and used Siphunculata (Anoplura) for comparative purposes. His results confirmed the earlier work of Mjöberg, who had pointed out the marked resemblance between the Siphunculata (Anoplura) and the less specialized forms of the Mallophaga. In the same year Müller (1915:29-32) described and figured the respiratory system in the clothes louse.

In the hog louse there are fourteen stigmata, the typical number for Siphunculata (Anoplura) — one pair on the thorax in line with the second pair of legs, and six pairs on segments 3 to 8 of the abdomen. The abdominal stigmata on segments 3 to 6 lie on the dorsal transverse median line, while those on segments 7 and 8 are more posterior and lateral in position and can be seen from both dorsal and ventral aspects. The stigmata are slightly raised above the integument and are surrounded by a stout chitinous band, the peritreme. The thoracic stigmata are oblong-ovate, measuring from 0.06 to 0.07 millimeter at the widest part, and the abdominal stigmata are circular, with a diameter of about 0.05 millimeter.

The respiratory system (Plate LIX, 1) consists of two lateral tracheal trunks extending the whole length of the insect, a posterior abdominal commissure, and four more slender commissures in connection with the main ganglia. In the abdomen the main tracheae lie near the dorsal surface on either side of the alimentary tract, and are united posteriorly in segment 8 by a commissure of diameter equal to their own, from which numerous fine branches pass to the fat cells of segment 9. In segments 8 to 3 a branch is given off from each main trunk to the stigmata of the segment, and they in turn each send off two slenderer branches which,

breaking up into innumerable tracheoles, pass through the lateral muscles and support the digestive and reproductive organs from their ventral aspect. Between segments 7 and 3, eight branches are given off centrad from the lateral trunks. These pass to the dorsal muscle plate, the heart, the dorsal fat cells, and the surface of the alimentary tract.

In some species, roots of branches extending laterad from the main trunks, between the branches to the stigmata of segment 3 and the thorax, have been described by investigators who have regarded them as vestiges of branches to the lost stigmata of segments 1 and 2. Such roots have not been found in this case. In the region of the second segment two slender branches are given off, one laterad and the other centrad. The former soon bends downward and breaks into numerous tracheoles on the surface of the salivary glands, while the latter ramifies among the fat cells on the dorsal anterior region of the stomach. Under the sternite of the first segment a slender branch comes off from each main trunk and passes to the dorsal surface of the stomach, and a second fine branch arises where the main tracheae bend somewhat ventrad as they pass into the thorax. This branch breaks up in the thoracic muscle of the third pair of legs.

In the thorax the main tracheae bend underneath the muscles coming from the legs to the metathoracic apodeme. In line with the third pair of legs a very short branch is given off laterad, from the posterior side of which arise two branches, one passing directly into the leg, and the other centrad for a short distance, when it divides into three parts. The first part of this branch is the commissure of the metathoracic ganglion, the second ramifies on the ventral wall of the stomach, and the third bends laterad passing into the leg. Opposite the second pair of legs is a tracheal plexus, from which spread six large branches as well as many small branches supplying the surrounding muscles and fat cells. A stout dorsal branch connects the plexus with each thoracic stigma. The first branch going cephalad divides, one part passing laterad to the first pair of legs, the other passing centrad as the commissure of the prothoracic ganglion, first giving off a branch which turns backward and also enters the first pair of legs. The second branch going cephalad is a continuation of the lateral tracheal trunk and passes to the head. A branch passes directly centrad as the commissure of the mesothoracic ganglion, and from it a branch arises at the lateral border of the ganglion and bends

around, passing into the second pair of legs. The fifth branch leaves the plexus almost at the same point as the preceding, turns back, and enters the main trunk centrad of the point of issue of the tracheae of the third pair of legs, thus forming a loop, which may correspond to the thoracic tracheal triangle described by Harrison (1916 a:105) in some Mallophaga. There, however, the thoracic stigma forms the apex of the triangle, while this loop lies behind the stigma. Harrison suggests that the inner side of the triangle may be the only survival of wing tracheae. The sixth branch comes from the branch to the thoracic spiracle just dorsad of its entrance into the main trunk, and passes into the second pair of legs. As has been shown, two tracheae pass into each leg, one of which lies ventral and the other dorsal. In the coxae, branches are given off which break up into many fine tracheoles; in the femur a large branch is given off from each trachea, and one of these branches passes along with the main branches into the tibia, where the latter subdivide many times, passing into the spur, the pad, the tarsus, and the claw.

The main trunks, on leaving the tracheal plexus, bend centrad and dorsad, passing into the head on either side of the esophagus and the aorta directly under the occipital apodeme. Just behind the sub-esophageal ganglion they diverge, and shortly give off a lateral branch to the neighboring muscles. Behind the brain a branch is given off centrad, and from its root the commissure of the sub-esophageal ganglion issues, while it passes forward close to the lateral borders of the brain. The main trunks continue forward alongside the antennal nerves, give off a branch to each antenna, and break up into numerous branches among the glands, the fat cells, and the sensory cells of the anterior region of the head.

The external surface of the stigma resembles a cart wheel with an open hollow axis, and sections show the vestibule between the stigma and its trachea to be filled with hair-like, chitinous structures radiating from its inner surface to a thin wall surrounding a slender central canal (Plate LIX, 3). These spoke-like projections doubtless prevent the entrance of foreign particles along with the air. A similar structure has been described by Müller (1915:30) in the clothes louse. Between the vestibule and the trachea is inserted the closing apparatus, concerning the mechanism of which there is still some uncertainty. Krancher (1881:522–533) briefly described the structure in *Haematopinus suis*. His figure shows the nature of the vestibule, the closing lever, and one intrinsic muscle between

the free end of the lever and the wall of the trachea opposite the attachment. No further description appeared until that of Mjöberg (1910:221), who figures a single muscle attached to the free end of the lever, and describes its insertion in the body wall near the stigma. At the close of a detailed study of the stigmata of Heteroptera and Homoptera, Mammen (1912:172) divides insect stigmata into four groups, according as they have one extrinsic muscle, one intrinsic muscle, two muscles, or three muscles, connected with the closing apparatus. Harrison (1916 a:116) gives a brief résumé of the literature on the subject. He finds in Siphunculata (Anoplura) and in Mallophaga two muscles, which may be homologous with the "Musculus constrictor" and the "Musculus tendinosus" described by Solowiow (1909:707) in the caterpillar of *Cossus cossus* L. Müller (1915:30) refers to Landois' work on Phthirius, and says that he himself could get no clear picture of the structure in *Pediculus vestimenti* from the study of sections.

Study of the hog louse has revealed a closing apparatus resembling that of *Heterodoxus longitarsus* as figured by Harrison (1916 a:116), who describes it as an intermediate type and gives no account of the musculature. The thoracic and abdominal stigmata are essentially the same in structure and in mechanism, but the vestibule of the thoracic stigmata is somewhat shorter, measuring approximately 0.08 millimeter from the surface of the stigma to the closing lever, while that of the abdominal stigmata (Plate LIX, 3) measures 0.11 millimeter. The approximate diameter of the vestibule of the abdominal stigmata is 0.03 millimeter, and at its inner end it narrows and both walls become strongly chitinized. A chitinous lever about 0.03 millimeter long is attached to the ventral wall, and the dorsal wall projects into the lumen as a sharp point. Beyond the lever the wall continues strongly chitinized and somewhat convex for a distance of about 0.016 millimeter, when it passes into the trachea proper. This region corresponds to the bulla of Harrison. In gross dissections no muscles have been found (Plate LIX, 2), but from the study of sections cut at various angles there appear to be two muscles arising from the free end of the lever. One of these is inserted in the convex wall of the bulla, and the other in the body wall just dorsad of the stigma. This agrees with the findings of Harrison in other Siphunculata (Anoplura) and in the Mallophaga. He offers two interpretations of the structure: (1) both the extrinsic and the intrinsic muscle function in closing the

stigma, or (2) closing is effected by the intrinsic muscle and reopening by the extrinsic muscle. With Harrison, we consider the former the more reasonable explanation, in which case it is assumed that the trachea opens through its own elasticity on the relaxing of the closing muscles.

THE MUSCULAR SYSTEM

With the exception of Osborn's (1904) note on the musculature of the protrusible disks and the claw, nothing has been published concerning the muscular system of the hog louse, and the only work on an allied species is that of Ströbelt (1882, English trans. 1883:100) on *Linognathus vituli* (*Haematopinus tenuirostris*). Landois (1864:22, 1865 a:33, 39, and 1865 b:495) described and figured a part of the musculature of the species affecting man, and was the first to observe the arrangement of the muscles in the female. Recently Müller (1915:10) has confirmed the work of Landois and has described in addition the arrangement of the muscles in the male. Nuttall (1917 a:295) has briefly mentioned and summarized the different arrangement of the abdominal muscle plates in the two sexes as described by Landois and Müller. The musculature of the hog louse presents some striking contrasts to that of the pediculi infesting man.

The head contains many muscles, of which the majority control the pharynx and the mouth parts and are described later in connection with those parts. The muscles controlling the antennae are confined to the head and the first segment of the antennae, those in the head all originating in the dorsal wall and none of them in the ventral as in the pediculi infesting man. There are six muscles, which originate in close succession on either side of the dorsal median line above the frontal ganglion and immediately posterior to the elevator muscles of the pumping pharynx. The two anterior muscles pass obliquely backward and downward, and are inserted in the ventral articulation of the antennae with the head; the two median muscles pass almost directly ventrad and are inserted in the dorsal articulation of the antennae with the head; and the two posterior muscles pass obliquely anterior and downward and are inserted immediately posterior to the median muscles. In the antennae the muscles are confined to the first segment, and consist of four bundles originating at the articulation of the antennae with the head and inserted two in the anterior and two in the posterior articulation of segments 1 and 2.

The muscles controlling the movements of the head lie in the anterior part of the thorax and have their origin in the metathoracic apodeme and in the strongly chitinized tergite of the prothorax. The elevator and retractor muscles are six in number and originate in the metathoracic apodeme, three on either side of the median line; the two median muscles are inserted in the distal ends of the occipital apodeme, and the two lateral muscles on either side pass cephalad and are inserted in the neck. The two depressor muscles are made up each of three strands, and originate in the dorsal wall of the prothorax on either side of the elevator muscles on the transverse median line of the first pair of legs. They pass obliquely ventrad and cephalad, and are inserted as two short, stout tendons in the chitinous ring of the neck on either side of the ventral median line. The lateral movements are controlled by muscles made up each of four strands. They originate in the dorsal wall of the prothorax laterad of the depressor muscles, and pass obliquely centrad, where they are inserted in the lateral borders of the prongs of the occipital apodeme at its distal end.

The muscles controlling the legs originate in the metathoracic apodeme, and if the dorsal surface of the thorax be carefully removed or if horizontal sections be made through this region, the muscles are seen to have a stellate arrangement with the apodeme as the center point of the star. A similar condition exists in the pediculi infesting man, and has been figured by Müller (1915). There are in all eighteen groups of muscle strands originating in the apodeme, and three of these groups are inserted as stout tendons — two in the dorsal articulation of the coxa with the thorax, and one a short distance within the ventral wall of the coxa, in each leg. Each group is composed of some five to seven strands, which vary in length according to their point of origin in the apodeme. The muscles passing to the first pair of legs are also supported by the apodeme, which passes from the prothorax to the prosternum, and if this be dissected out it is seen to pass through some of the individual strands of the bundles.

On the ventral surface of the thorax there is no muscle plate resembling that of the pediculi infesting man, but two transverse muscle bundles, passing, respectively, between the ventral borders of the coxae of the second and third pairs of legs, are present and correspond to the intercoxal muscles described by Müller. The anterior band consists of four strands, and in these are inserted the posterior arms of the apodeme of the prothorax

nd prosternum. It lies just anterior to the stomach, below the esophagus, nd is covered ventrally by the thoracic ganglia and many fat cells. The osterior band consists of two strands and passes across the ventral ırface of the stomach. From each of the points of its insertion in the ɔxae of the third pair of legs, a muscle passes somewhat obliquely cephalad, nd these muscles are inserted in the posterior arms of the apodeme here they enter the anterior transverse muscle band. In sections made ırough lice having the stomach filled with blood, the transverse muscle ands appear to be imbedded in the stomach, owing to its walls having ecome distended on either side of them.

The work of Landois and of Müller has made known the great difference ı the longitudinal abdominal musculature of the two sexes of the manıfesting louse, and Nuttall (1917 a:296) has summarized this difference s follows:

	Dorsal abdominal muscles are present under segments	Ventral abdominal muscles are present under segments
the male	2, 3, 4, 5, 6, 7, 8	2 + 3, 4, 5, 6
the female	6, 7, 8	2, 3, 5, 6

ı the hog louse no such difference is found. In both sexes a dorsal uscle extending the whole length of the abdomen is present. It consists some eight muscle strands on either side of the median line. In segment these strands converge to the point of their attachment to the posterior ırface of the metathoracic apodeme, and posteriorly, in segments 8 and the two halves of the plate diverge and the heart lies between them. he contraction of the muscle plate raises the posterior end of the abdomen. ı both sexes the ventral muscle plate (Plate LIX, 4) begins in the anterior ɔrder of segment 2 and extends caudad to the posterior border of segment

The number of strands in each segment is apparently not arbitrary, ıd the following have been found most frequently:

	Number of strands in male	Number of strands in female
Segment 2,	12 central and 4 lateral	10 central and 4 lateral
Segment 3,	14	18
Segment 4,	14	16
Segment 5,	14	16
Segment 6,	14	16

In segment 2 the four lateral strands frequently appear as three, because the two outermost fuse almost immediately after leaving their attachment between segments 2 and 3. At their proximal end these lateral strands are attached to the lateral body wall a short distance cephalad of the anterior border of the pleurite of segment 3, and at their distal end, when looked at from their ventral aspect, the innermost strand and a part of the next innermost are seen to underlie the three outermost of the central strands. The dorsal and ventral muscle plates are composed of segmental muscles in which the attachment between those of the successive segments has become stronger than their attachment to the intersegmental folds of the body wall, so that the dorsal and ventral muscles can be dissected off as entire muscle plates.

While the two sexes bear a close resemblance in the longitudinal musculature of the abdomen, they show a marked contrast in the dorso-ventral musculature. In the male the digestive and reproductive organs occupy only the center of the abdomen, but in the female the ovaries occupy most of the lateral regions as well. In the male there is a powerful dorso-ventral musculature, which not only assists in respiration but plays an important part in the act of copulation. That part of each of segments 2 to 8 between the alimentary canal and the lateral body wall is filled with stout blocks of muscle, definite in number and arrangement for each segment (Plate LIX, 5). In segment 2 there are two blocks of muscle, in segments 3 and 4 eight blocks, in segments 5, 6, and 7 nine blocks, and in segment 8 eight blocks. The tracheae from the stigmata to the lateral trunk pass between these blocks of muscle, and between the muscle and the lateral body wall lie numerous fat cells. In segment 9, where the muscles controlling a part of the copulatory apparatus originate, there are no dorso-ventral blocks of muscle.

In the female there is a deep lateral indentation between the successive segments from 3 to 8, that between segments 6 and 7 being somewhat deeper than the others. Internally these indentations have the appearance of pillars or sections of the cuticula which divide the lateral parts of the successive segments into a series of small chambers. At the end of each cuticular pillar two bands of muscle are attached to the dorsal and ventral walls of the abdomen, and these curve close to the centrad wall of the pillar. In segments 4, 5, 6, 7, and 8, in the anterior half of the segment

there is a moderately stout band of muscle which is attached to the dorsal and ventral cuticula between and in line with the bases of the pillars. Within the lateral chamber of each of segments 3 to 8 there is a group of five slender muscle strands, and in segment 9 there are six larger strands. On the ventral surface these delicate strands are attached to the body wall just below the strongly chitinized pleurite, and from there they pass somewhat obliquely centrad and dorsad to the cuticula just within the central border of the chamber.

The leg muscles are similar in both sexes and show no unusual modifications except in those controlling the claw. Landois (1865 a:33 and 1865 b:495) studied in part the leg muscles of the man-infesting pediculi, and Müller (1915:14) has figured the muscles of the leg of a female clothes louse. As already said, Osborn (1904) described the musculature controlling the tarsus and claw of the hog louse. There are four muscles in each coxa, which originate in its articulation with the thorax and are inserted in its articulation with the trochanter. Within the latter are the flexor and extensor muscles of the femur, with their origin and insertion in its proximal and its distal articulation, respectively. The flexor muscle of the tibia is made up of a number of fibers which originate at intervals along the dorsal wall of the femur and come together in one tendon for their insertion in the ventral line of the articulation of the femur with the tibia. The extensor muscle is made up of two bundles of fibers originating in the articulation of the trochanter with the femur and in the proximal dorsal wall of the femur; it ends in two tendons which are inserted in the articulation of the femur with the tibia on the dorsal side of the leg. In the tibia there is one large muscle, made up of a number of closely set fibers which originate in the proximal posterior and ventral walls of the tibia. The muscle passes along the whole length of the segment, midway giving off a branch which is inserted in the base of the protractile disk. On entering the tarsus the muscle becomes a tendon which ends in a strongly chitinized process of a diameter somewhat greater than that of the tendon itself. It is inserted in the ventral wall of the tarsus under the base of the blunt process situated there, so that its anterior end lies just within the border of the claw and is attached to its ventral curve. The position and attachment of this muscle has been determined from the study of mounts of gross specimens and from numerous dissections of legs. It must be regarded as the extensor muscle of the claw, and the

branch going to the disk must be the retractor muscle of the disk. Osborn figured this large muscle lying in the tibia as inserted in the dorsal wall of the tarsus, and a continuation passing from there to the dorsal curve of the claw. He also figured a flexor muscle of the tarsus. Neither of these two conditions has been found in the present investigation, and the absence of flexor muscles of the tarsus and the claw may be explained on the following grounds: the tarsus becomes defined as a segment distinct from the tibia only after the final molt, and is then practically immovable, while the claw in its normal resting position is bent over with its tip touching the ventral anterior extension of the tibia, so that only an extensor muscle is necessary for its function. No mechanism for ejecting the protractile disk has been found, and, as Osborn suggested, this ejection may be accomplished by means of an elastic framework.

The foregoing account deals only with what may be called the skeletal muscles of the louse. The muscles controlling the various systems of the body are described later in their respective connections.

The histological structure of the muscle is best seen in the material fixed in Bouin's solution and stained with Mallory's anilin-blue connective-tissue stain, when all the cross-striations stand out with great clearness. All the muscles have a well-developed sarcolemma and are richly supplied with peripheral nuclei.

THE VASCULAR SYSTEM

In the writings of the early investigators of the Pediculidae, no real description of the dorsal vessel is to be found. Landois (1864:11), after many attempts, distinguished in freshly molted insects a slender tube originating in the region of the transverse tracheal band. He traced it cephalad to the middle of the abdomen, but could follow it no farther. Its pulsations were more rapid than those of the stomach. Mjöberg (1910:223) pointed out the similarity of the heart in the two groups which he studied, and drew attention to the lack of any thorough work in the Siphunculata (Anoplura). According to Schröder (1912-13:390), Provazek in 1905 described and figured the heart of *Haematopinus spinulosus* Burm., and this appears to be the first anatomical description of the heart of a siphunculatan. Müller (1915:27) has figured the heart of the clothes louse in gross and in sections, and has described in detail its anatomy and its pulsations in living specimens. Harrison (1916 b:220)

again called attention to the similarity of the heart in Mallophaga and Siphunculata (Anoplura), and referred to Fulmek's (1905) work on Mallophaga, in which there is a short résumé of the literature of the heart, beginning with the work of Wedl (1855), who first distinguished in the dorsal vessel a posterior, specially contractile part — the true heart — and an anterior, more vessel-like part — the aorta.

In the hog louse the heart lies in the two posterior abdominal segments, between the halves of the dorsal muscle plate, and is attached to the dorsal wall on either side of the median line by two delicate septa. It is oblong-ovate, measuring approximately 0.38 millimeter in length and 0.075 millimeter in breadth, and has two lateral indentations on either side which give it a three-chambered appearance (Plate LIX, 6). Attached to the lateral and ventral surfaces are three pairs of wing muscles which pass directly laterad under the two halves of the dorsal muscle plate and are inserted in the lateral body wall toward the ventral surface. To the central wing muscles on either side is attached a group of six pericardial cells similar to those described by Fulmek (1905:620) in *Nirmus* sp. In gross dissections the ostia cannot be clearly seen, but sections show three pairs, lateral in position. Anteriorly the heart leads into the aorta, which lies free throughout most of its length in the body cavity and passes cephalad entering the head alongside the esophagus. Its width varies from 0.03 millimeter at the posterior end to 0.02 millimeter at the anterior end. In some few cases it seemed swollen to a bulb in the region of segments 6 and 5, but we did not find this to be a constant character.

The wall of the heart is very thin, and in section it is seen to be of uneven thickness (Plate LIX, 7). Its histological elements appear to be mostly muscular, and, while nuclei are visible, they resemble those of the sarcolemma rather than those of a true epithelium. Where the wall is slightly contracted, it has a false appearance of being toothed. Where the heart passes into the aorta there is a succession of six pairs of valve-like structures extending from opposite walls of the aorta into its lumen and almost meeting on the median line. Sections showed no definite structure that would reveal the true histological nature of these.

The blood is a colorless fluid and its cells can be seen singly and in groups scattered throughout the heart and the aorta. They are definite round cells with a well-defined central nucleus, and do not appear to be

numerous. Owing to the thickness of the cuticula it is impossible to watch the pulsations of the heart in living specimens, as was done by Landois (1864:11) and by Müller (1915:29) in the clothes louse.

The most successful preparations of the dorsal vessel have been obtained by first removing the dorsal cuticula of the whole abdomen and then the dorsal muscle plate. If the posterior attachment of the muscles of segment 9 be carefully loosened, the heart and its wing muscles will generally be found intact on the ventral surface of the muscle plate.

THE NERVOUS SYSTEM

Since the time of Swammerdam (1682, English trans. 1758:36), it has been known that lice possess three large thoracic ganglia and no abdominal ganglia, and that nerves pass backward from the metathoracic ganglion over the ventral stomach wall. It was not, however, until almost two hundred years later that a more detailed description of the central nervous system appeared, when Landois (1864:24) published his description of *Phthirius inguinalis*. He referred to Swammerdam as correctly describing three thoracic ganglia, and to Burmeister (1847) as incorrectly describing two in the Pediculidae. He figured the brain, the connectives, and the thoracic ganglia, but showed neither a sub-esophageal ganglion nor a sympathetic system. In his study of *Pediculus vestimenti*, published a year later (Landois, 1865 a:54), he found no noteworthy difference between the species. Brühl (1871:477) devoted his attention chiefly to the study of the peripheral ganglia, which he described as " Haar-Gehirne " and of which he counted approximately one hundred and fifty on each louse. Graber (1872:165) reviewed the work of Landois, and described the connectives between the brain and the thoracic ganglia as being at least four times the length given by Landois. On one occasion he found and figured a pear-shaped ganglion with two nerves passing backward from it. He thought it was the hitherto undescribed sub-esophageal ganglion, but, since it lay on the dorsal surface of the esophagus, he concluded that it must be a part of the visceral nervous system. Mjöberg (1910:222) did no work on the nervous system, but in a short note he mentioned the concentration of the ganglia in the thoracic region and the lack of any detailed work in both Siphunculata (Anoplura) and Mallophaga. A considerable advance has been made by Müller (1915:32–37) in his

description of the nervous system of the clothes louse, and he has called attention to the fact that, although in the mature louse the ganglia are concentrated in the thorax, in the embryo figured by Cholodkovsky (1903: 124) they extend some distance into the abdomen.

The central nervous system of the hog louse consists of five ganglia, their connectives, and commissures, and its approximate length from the anterior border of the brain to the posterior border of the metathoracic ganglion is 0.93 millimeter (Plate LIX, 8). The supra-esophageal ganglion lies in the posterior half of the head behind the level of the insertion of the antennae. It is a large, compact ganglion, deeply grooved anteriorly and surrounding the dorsal and lateral surfaces of the esophagus like a collar; its position is somewhat oblique, and the three segments of which it is composed are very closely fused. Its anterior lobes are joined on the ventral surface by the esophageal commissures, which can be easily seen in sections but are invariably broken in the process of gross dissection. These commissures were seen also by Müller (1915:34) in the clothes louse, and he suggested that they be named the "Commissura cerebri subpharyngealis." From the tritocerebron a pair of nerves pass out anteriorly and soon divide, one branch of each going to the frontal ganglion and the other to the labrum, where each subdivides into at least four branches terminating in large multinuclear sensory cells from which slender processes pass to the anterior wall of the head on either side of the haustellum. The ventral anterior part of the deutocerebron forms the olfactory lobes. In gross dissection these could not be distinguished, but they were found in series of longitudinal sections through the head, and from each a large nerve passes to the antennae. These nerves lie dorsad and somewhat laterad of the nerves from the tritocerebron. The optic lobes, also indistinguishable from the mass of the brain, send nerves out to the eyes, which are situated on prominences behind the antennae, are poorly developed, and are without pigment. The sub-esophageal ganglion is concealed anteriorly by the protocerebral lobes of the brain, and the esophageal connectives are so short as to be invisible unless the brain be raised. It is a heart-shaped ganglion, broadest anteriorly, and having a small indentation in which the esophagus rests. In sections, three pairs of nerves can be seen passing from it to the mouth parts.

From the apex of the sub-esophageal ganglion two closely apposed connectives pass backward along the median line to the prothoracic

ganglia. They measure approximately 0.22 millimeter in length. The thoracic ganglia are large and broad. Their approximate length is 0.38 millimeter and width 0.28 millimeter. They are closely fused, showing neither connectives nor commissures, but both in gross specimens and in sections it is evident that each ganglion has arisen through lateral fusion of two ganglia. They lie in the most anterior part of the thorax, and when the stomach is distended their position is oblique dorso-ventral rather than ventral. All three send out lateral nerves to the legs and the thorax, and the metathoracic ganglion sends in addition eight nerves to the abdomen, of which the two nearest the median line are the largest. These nerves pass backward to the ninth abdominal segment and give off in their course many slender branches to the visceral and reproductive organs.

The sympathetic system is well developed. The frontal ganglion is somewhat pear-shaped and lies some 0.03 millimeter in front of the brain, on the median line above the junction of the pumping pharynx with the true pharynx. Slightly laterad on either side of the ganglion a small nerve is given off anteriorly from the branches connecting the ganglion with the brain. The course of these nerves has not been seen, but they may connect the frontal ganglion with two smaller ganglia which are united to each other and lie on the median line above the anterior part of the buccal plate of Harrison (Plate LX, 1). Similar ganglia have been seen by Sikora (1916:28) in the clothes louse, and she has suggested that they are homologues of the prefrontal nerve plexus described in other insects. From the anterior end of the frontal ganglion a nerve passes forward on the median line, and from it numerous lateral branches are given off. From the posterior end of the frontal ganglion the recurrent nerve runs back, passing under the brain close to the dorsal surface of the esophagus and finally terminating in the thorax in a small ganglion situated above the entrance of the esophagus into the stomach. From this ganglion at least two slender nerves pass backward over the dorsal stomach wall.

Both in gross dissections and in the study of serial sections, two subcircular structures, of a diameter approximating 0.03 millimeter, have been found under the protocerebral lobes of the brain. They are made up entirely of ganglion cells, show no central substance, and stain more deeply than the surrounding tissues. In no case has any connection

been traced between them and the brain, but they are in close association with the tracheoles of the commissure passing under its posterior part. While a study of the texts of Berlese (1909:588) and Schröder (1912–13: 86) suggests that these bodies may be homologues of the "corpora allata" described by Carrière and Bürger in 1897, Heymons in 1899, Janet in 1899, and others, a knowledge of their development is essential for their correct interpretation. A short distance behind the brain and approximately above the esophageal ganglion, there has been seen in longitudinal sections of the head a ganglion in the course of the recurrent nerve, but no branches have been found issuing from it. This may be the hypocephalic or hypo-cerebral ganglion figured by Berlese (1909:596).

No attempt has been made to interpret a peripheral nervous system such as was described by Brühl (1871:477) in the pediculi infesting man, but if the nerve to the antennae be followed, it is seen to give off branches to the second and third segments which end directly under the cuticula in large multinuclear sensory cells similar to those at the termination of the labral nerves. In the terminal segment the nerve breaks up into branches corresponding in number to the blunt spinelike processes on the terminal sensory plate. Each branch terminates under its process as an oblong-ovate multinuclear sensory cell (Plate LIX, 9), but the actual connections between the cells and the processes have not been seen. Similar sensory cells have been seen in a few sections underlying the hairs of the abdomen.

THE STOMODAEUM, MOUTH PARTS, AND SALIVARY GLANDS

Writing of the clothes louse, Sikora (1916:22) says: "Es gibt kaum ein anderes Insekt, über dessen Anatomie so lange gestritten wurde, und über das so viele voneinander gänzlich abweichende Meinungen geäussert worden wären, wie die Laus." Most of the literature is the outcome of investigations of the man-infesting pediculi, but in some instances more or less detailed comparative studies have been made on the hog louse. With a few exceptions workers have confined themselves to the study of the mouth parts and their homologies, and this for two reasons: first, because in the middle of the last century a controversy was carried on as to whether lice possessed biting or sucking mouth parts, and secondly, because the systematic position of the group, long a matter of uncertainty, was thought to be dependent on the morphological

interpretation of the mouth parts. Owing to the specialized nature of the mouth parts and the lack of any ontogenetic proof of their homologies, various interpretations have been offered by investigators according to their views of the affinities of the group.

The early naturalists of the latter half of the seventeenth century attributed sucking mouth parts to lice, and based their opinions on the experimental feeding of captive lice on themselves. Nitzsch (1818:304) confirmed the observations of Swammerdam as to the presence of a bristle sheath (not the true sheath, but the proboscis), and put forward the hypothesis that the inner tube of suction consisted of several setae. His drawings of the structure were published, not with the text, but posthumously by Burmeister (1838). A year later Erichson (1839:377) stated that previous workers had erred in their descriptions, and that the louse possessed no hooks on the haustellum but did have a pair of strong, four-jointed palpi and very distinct mandibles. This statement led to Burmeister's (1847) paper upholding and confirming the opinions of Nitzsch, in which he gave an account of the structures in the hog louse. His work, though in the light of more recent investigations incomplete and in parts inaccurate, was a distinct addition to the knowledge of the subject. It was followed the next year by a contribution from Simon (1848:274), who, in his treatise on skin diseases, described his joint work with Erichson and corroborated Erichson's statements as to the presence of true palpi and mandibles and the absence of a sucking apparatus.

The controversy was finally settled in 1864, when Schjödte (1864, English trans. 1866:213) published the results of his investigations and his interpretations of the artifacts which had misled the supporters of the biting-mouth-parts theory. In the same year Landois (1864:3) described the mouth parts of Phthirius as corresponding very closely with Erichson's and Simon's descriptions of those of *Pediculus capitis* and *P. vestimenti*, but when he published the results of his investigation of the clothes louse (Landois, 1865 a:34) he stated that his first interpretation was wrong and that the mouth parts were of the sucking type. Brühl (1871) described the mouth parts of the three species affecting man, and along with Schjödte considered the piercing mouth parts as having arisen through a modification of the mandibles and the maxillae, a view which, according to Enderlein (1905:631), originated in 1853 with Gerstfeldt, who regarded the mandibles as a tube made up of two halves and the

maxillae as the bristles lying within it. Graber (1872:138) distinguished in the mouth parts of Phthirius an upper lip, an under lip (proboscis), and a sucking tube formed possibly by the fusion of the mandibles and the maxillae and capable of protrusion from the proboscis, but he did not realize the true nature of the piercers and their sheath. He saw these structures extending far back in the ventral region of the head, and interpreted them as the retractor muscle of the proboscis.

The next two in the long succession of publications appeared at intervals of ten years, and both dealt, one entirely and the other in part, with species affecting domestic animals. Ströbelt (1882, English trans. 1883:86) described very incompletely some of the structures surrounding the mouth openings of *Linognathus vituli* (*Haematopinus tenuirostris*) without seeing the real mouth parts, while Meinert (1891–92:58) used *Haematopinus suis* to illustrate his study of the mouth parts of *Pediculus humanus* and figured the different parts of the apparatus. Meinert called the whole structure the pharynx, distinguishing the anterior part of the stomodaeum proper as the epipharynx and the ventral sheath and piercers as the hypopharynx.

A third decade passed before another contribution appeared, and then Cholodkovsky (1903:120) attacked the subject from a different aspect. Realizing the uncertainty pervading all the earlier literature—most of which had appeared before the application of section-cutting to investigation methods—as well as the urgent need of embryological studies to supplement the early work of Melnikow (1869:153), Cholodkovsky not only studied mature species of Pediculus and Haematopinus, but also many mounts and serial sections of different stages of embryos of two of the species infesting man. The result led him to believe that mandibles and maxillae are present in the early stages of the development of the germ band but disappear entirely before the escape of the young insect from the egg, and that the piercer sheath and its apparatus are formed from the labium alone. Melnikow (1869:153) had emphasized the relationship between the Mallophaga and the Pediculidae, and considered both as a family of the Rhynchota. Cholodkovsky agreed with the first part of this statement, but thought the two groups should rather be classed with the Orthoptera (particularly with Pseudoneuroptera), or, preferably, should be placed in a separate order by themselves, for which he suggested the name Pseudorhynchota.

This suggestion was criticized by Enderlein (1904:121 and 1905:626), who believed that these insects were hemipterous in their affinities, and consequently homologized the piercing apparatus with the maxillae, hypopharynx, and labium of the Rhynchota. His method of investigation was by gross dissection and by the study of cleared and mounted specimens. He used a number of related forms but gave the most detailed work to the interpretation of the hog louse. He compared the "mandibles" of the latter with those of the Corixidae, a proceeding which led to a discussion of the question by Handlirsch (1905:668), who emphasized the much clearer resemblance existing between the mandibles of the Siphunculata (Anoplura) and of different species of Mallophaga as figured by Snodgrass (1899). One outcome of the controversy between Cholodkovsky and Enderlein was the publication by Pawlowsky (1906:156) — a pupil of Cholodkovsky — of a résumé of the literature up to his time on the mouth parts of lice, and a description of the anatomy of the piercing and sucking apparatus of the Pediculidae.

Mjöberg (1910:203) made no study of the mouth parts but confined himself to a brief summary of the work of others, dealing at greatest length with Enderlein's work on the hog louse and his interpretation of the mandibles. Patton and Cragg (1913:531) gave an account of the mouth parts of *Pediculus vestimenti* "prepared, with the assistance of the above papers [of Enderlein and Pawlowsky], from sections and dissections." This account included also a description of the first part of the alimentary canal. The fact that the man-infesting pediculi are an etiological factor in the transmission of certain diseases has led to the publication within the last few years of three detailed papers on the anatomical structure of the anterior part of the alimentary canal and of the mouth parts proper. Those of Harrison (1916b) and Sikora (1916) appeared almost simultaneously, and that of Peacock (1918) some two years later. Owing to war conditions the work of Sikora was not available to the other two investigators, nor their work to her. Harrison and Peacock confined their investigations to the species affecting man, while Sikora introduced several species, among them the hog louse, for purposes of comparative study.

The head of the hog louse is most strongly chitinized on the lateral regions, and the chitinization extends a little way beyond the borders of both dorsal and ventral surfaces. The remainder of the ventral surface is only weakly chitinized, and at the anterior end the integument is

capable of considerable wrinkling; while the dorsal surface is strengthened by three rigid transverse areas, one in the region of the clypeus, a second between the bases of the antennae, and a third above the anterior part of the brain. At rest the mouth opening is a longitudinal slit and is not visible from the dorsal surface. At the anterior border of the head on either side of the mouth opening are two strongly chitinized areas, which extend a little way onto the dorsal surface of the head but considerably farther onto the ventral surface, and on each of which are situated two pairs of bristles (Plate LX, 2–4). Sikora (1916:13) found in the six species of lice she studied — *Pediculus vestimenti*, *Haematopinus suis* and *H. eurysternus*, *Polyplax spinulosus* (End.), *Haemodipsus ventricosus* (End.), and *Trichaulis vituli* (End.) — a paired chitinous structure having the form and size of mandibles, situated between the upper and lower lips and apparently adapted for biting or rasping. In sections made through the anterior head region (Plate LX, 1), structures corresponding in part to this description have been found, but they are apparently only very weakly chitinized and are not covered by an underlip. Their inner border is slightly serrated and they appear to be attached by slender muscles to the process on the inner lateral wall of the head with which the basal part of the "mandibles" of Enderlein are continuous. Whether these structures could play any part in feeding is uncertain.

The haustellum

Projecting in front of the anterior border of the head on the median line is a small tubelike structure, the haustellum. It is convex on the dorsal surface and has an open longitudinal slit, the buccal slit, on the ventral surface (Plate LX, 2 and 3). Its approximate length is 0.05 millimeter and width 0.03 millimeter, and its chitin is continuous externally with that of the head and internally with that lining the food canal. In the interior of the haustellum are four pairs of double teeth arranged in two longitudinal parallel rows. They are present in both young and mature lice and are known as the buccal teeth. At the inner end the haustellum is connected by a fold of soft cuticula with the buccal plate.

The buccal plate

The buccal plate (Plate LX, 2 and 3) is a strongly chitinized structure identical in width at its anterior end with the haustellum and at its

posterior widest part measuring 0.08 millimeter across. It has the shape of a capital A in which the crossbar is a slight curve, convex toward the apex of the letter, and on the dorsal surface the space between this curve and the apex of the letter is solid. Its total length from the anterior edge to the posterior end of the arms is approximately 0.22 millimeter. Laterally it curves downward and centrad, but the opposite sides do not meet, so that on the ventral surface there is an open slit continuous with the buccal slit. The posterior arms of the buccal plate are fused with the lateral wall of the pumping pharynx.

The pumping pharynx

The pumping pharynx (Plate LX, 2 and 3) is strongly chitinized on the ventral and lateral surfaces and is capable of considerable dilatation on the dorsal surface. Its width at rest is 0.06 millimeter and the combined length of the buccal plate and the pumping pharynx is 0.5 millimeter. Its ventral surface extends forward to the posterior end of the ventral slit of the tubelike part of the buccal plate, and its dorsal surface is continuous with that of the buccal plate. Toward the posterior end there is a somewhat knoblike projection of the lateral walls, followed by a rather short backward prolongation of the more strongly chitinized part at the junction of the pumping pharynx with the true pharynx.

The pumping pharyngeal tube

From the anterior end of the pumping pharynx, two half tubes (Plate LX, 1 and 2) pass into the groove of the buccal plate but do not extend quite to its anterior end. Their ventral edges overlie each other; their dorsal ends lie apart, but so close under the buccal plate that a tube is formed through which blood is drawn during feeding. This tube has been called by Harrison (1916 b:209) the "buccal tube," by Sikora (1916: 26) the " Haustellumhalbröhre," and by Peacock (1918:101) the " pumping-pharyngeal tube." The true nature of the connection between this tube and the pumping pharynx can be followed only in sections, and is discussed later.

The pharynx

The pharynx (Plate LX, 1 and 2) was called by Enderlein (1904:127) the " larynx," and he described it as a chitinous band bent around on itself over the esophagus and never fused with the pharynx (pumping pharynx).

In cleared specimens he evidently saw only the anterior, strongly chitinized band of the pharynx. It is a somewhat cone-shaped structure having its widest diameter, which is approximately 0.15 millimeter, a little posterior to its transverse median line. In sections its ventral aspect is seen to lie almost level along the median longitudinal line of the head, and its dorsal surface passes obliquely toward the top of the head. Between its transverse median line and its part of greatest diameter is a more strongly chitinized region crossing the dorsal surface as a band and passing obliquely and posteriorly down the sides to the ventral surface, where the two bands run backward for a short distance, each lying somewhat laterad of the median line (Plate LX, 3). Behind the muscle insertions is a second region of strong chitinization, followed by a sphincter muscle, behind which the diameter lessens until it passes as the slender esophagus under the brain.

The esophagus

The esophagus (Plate LX, 2 and 3) passes directly backward between the tritocerebral lobes of the brain, over the sub-esophageal ganglion, and into the thorax between the two main tracheal trunks. At the posterior end of the head the esophagus, the dorsal vessel, the tracheae, and the connectives between the sub-esophageal and thoracic ganglia, are inclosed by a wall of thin cuticula, which is continuous with and shows the same staining reactions as the cuticula separating the posterior end of the piercer sheath from the thorax. It is a structureless membrane (Plate LX, 5). At its posterior end the esophagus passes over the anterior part of the stomach lying in the thorax, and enters its dorsal surface under the tergite of the second abdominal segment. Its length from the posterior end of the true pharynx to its passage into the stomach is approximately 1.03 millimeters and its diameter 0.03 millimeter. In sections its wall is seen to consist of flattened epithelial cells lined by a thin chitinous intima, but no basement membrane can be distinguished. The usual muscle layers are present, but are so fine as to be distinguished only with considerable difficulty. At rest and empty, as it is seen in sections, the wall shows a number of small convolutions.

The "mandibles" of Enderlein

On either side of the pumping pharynx, where the posterior arms of the buccal plate fuse with its lateral walls, lie two triangular chitinous

structures (Plate LX, 2 and 3) which Enderlein (1904:127) interpreted as "mandibles" and Sikora (1916:16) as "dreieckige Skelettstücke." Just anterior to the posterior dorsal margin of each is a groove, and at its lateral end articulates a rodlike structure which, according to Enderlein (1904:128), is the basal part of the mandibles and articulates anteriorly with the lateral wall of the head. Serial sections of the head show this basal part passing directly into the chitin of the wall, but show no articulation of the parts, a condition which has been described also by Sikora (1916:13–14). At their central angle these structures are attached to the sides of the pharynx by a structureless tissue, but it has not been found possible to determine the exact nature of the connection.

Musculature of the stomodaeum

During the act of feeding, the stomodaeum is moved forward by protractor muscles, and by the forward movement of the buccal plate the haustellum is protruded and the buccal teeth are everted (Plate LX, 4). There are two pairs of protractor muscles, a dorsal pair originating in the anterior wall of the head and having their insertion in the posterior arms of the buccal plate, and a ventral pair originating in the posterior lateral angles of the "mandibles" of Enderlein and having their insertion in the ventral surface of the knoblike processes at the posterior end of the pumping pharynx (Plate LX, 2). By the contraction of these two pairs of muscles the whole pharynx is moved forward.

There are three pairs of retractor muscles, two dorsal and one ventral. The former originate side by side on the dorsal wall of the head, laterad of the pharynx and just posterior to the muscles passing from the median line of the dorsum to the antennae. Both pairs of dorsal retractor muscles are of approximately the same dimension, and pass forward to end, the outer pair as long, slender tendons inserted in the lateral walls of the pumping pharynx in the margin of its fusion with the posterior arms of the buccal plate, and the inner pair, which lie close to the lateral wall of the pharynx, as much shorter tendons inserted in the dorsal surfaces of the posterior knoblike projections on the lateral walls of the pumping pharynx. The tendons of these muscles were recognized as such by Meinert (1891–92:Pl. I, fig. 3), and represent the "fulturae" of Enderlein (1904:127). The ventral retractors originate in the latero-ventral wall of the head in the region of the anterior level of the brain.

They are somewhat smaller than the dorsal retractors, and are inserted as slender tendons in the ventral surface of the posterior knoblike projections of the lateral wall of the pumping pharynx.

In addition to protractor and retractor muscles, the pumping pharynx has six pairs of elevator muscles which originate in the dorsal wall of the head and are inserted in the flexible dorsal wall of the pumping pharynx. Four pairs of these muscles are slender. These originate somewhat laterad of the dorsal median line of the head, and pass rather obliquely centrad to their insertion in the median line of the pumping pharynx. The two remaining pairs of muscles, which are the second and fourth pairs in the succession from the anterior end, are much stouter. They originate in the dorso-lateral wall of the head and pass obliquely centrad to their insertion in the lateral edges of the two small chitinous plates imbedded in the roof of the pumping pharynx. Both their origin and insertion are distinctly laterad of those of the slender muscles. The frontal ganglion lies imbedded among these elevator muscles, and is protected laterally by the sixth pair, which, after their origin, pass rather obliquely backward for a short distance, until they meet the flexor muscles of the antennae, when they bend directly ventrad to their insertion in the posterior end of the pumping pharynx.

In the man-infesting louse, Harrison (1916b:213) describes two sphincter muscles, an anterior and a posterior, surrounding the pharynx; Sikora (1916:31) says there are many constrictors present; and Peacock (1918:105) describes an anterior, a medial, and a posterior sphincter. In this respect, as well as in the number and arrangement of the dilators, the pharynx of the hog louse is markedly different from that of the man-infesting louse. The whole structure is apparently covered with a layer of circular muscle, which varies considerably in thickness. Anteriorly, where the cuticula is only weakly chitinized, the muscle is well developed and surrounds the whole structure as a sphincter. Posteriorly, in the region of the first chitinized plate, the muscle is very thin except on the ventral surface, while in the region of the second chitinized plate it is thicker and on the median line sends off a number of strands which pass directly upward between the dilator muscles to the dorsal wall of the head. Before the pharynx passes into the esophagus the muscle layer assumes a moderate thickness throughout, and this part may be called the posterior sphincter. Only in its posterior

half is the wall of the pharynx capable of any dilatation, and there are inserted four muscles of which the two median are the largest. They originate in the dorsal wall of the head above the anterior lobes of the brain, and pass obliquely forward and downward to their point of insertion. Their contraction, while it may dilate the pharynx, would seem rather to draw it back to its resting position.

Between the eye prominences and the neck three bands of muscle originate in the lateral wall of the head. The median band extends farthest back and the ventral the next farthest, while the dorsal is the shortest. Just behind the antennae these bands unite in a common tendon which is inserted in the anterior lateral angles of the " mandibles " of Enderlein. In his first description of the mandibles (1904:128–129) Enderlein did not see these tendons, but in his second paper (1905: 629–630) he describes and figures them as the tendons of the mandibular flexors. He also figures tendons passing forward from the posterior lateral angle of the mandibles to the anterior wall of the head, and calls them the tendons of the mandibular extensor. Sikora (1916:16), however, describes these last as a uniformly thin strand passing from the ventral border of the triangular skeletal piece to the side of the underlip. In gross dissections the " mandibles " remain attached to the anterior wall of the head by this strand, but its true histological nature has not been determined, since it has not been identified in any of the series of sections made through the head. Enderlein found the " mandibles " well developed only in the hog louse, but considered that the finding of the muscle tendons removed every doubt as to their morphological interpretation. Sikora (1916:13, 17), on the other hand, reserves the term " mandible " for the already-mentioned structure lying between the upper and lower lips and adapted for biting or rasping. She calls the " mandibles " of Enderlein " gewölbten Chitinplatten " or " dreieckige Skelettstücke," and denies the possibility of their being mandibles on the ground of their position back in the head and their separation by the pharynx. She suggests two functions for them, namely, to draw the pharynx forward and to transmit to the true mandibles the motor impulse of the muscles. Since the " mandibles " are attached to the lateral wall of the pumping pharynx and the buccal plate, the contraction of the tendon muscles would exert a backward pull on their anterior angle, and they, working as a lever, would serve to push forward the buccal plate and the pharynx, a function performed

by the two pairs of protractor muscles. Sikora's second suggestion is based on the fact that she (1916:18) regards the basal part of the "mandibles" of Enderlein as the posterior articular processes of the true mandibles, which Enderlein (1905:637) in turn has interpreted as the ventral prolongations of the lateral sclerite. According to Enderlein these are pushed far under the scalelike labium and are covered by it ventrally. Sikora attributes the double function of opening the mandibles and moving forward the pharynx to the ventral protractor muscles, and their closing to the contraction of the tendon muscle. No constructive criticism of this interpretation is offered for the present, because it is believed that the final morphology of the parts can be determined only by embryological investigation.

The mouth parts

From the ventral surface of the stomodaeum at the junction of the buccal plate and pumping pharynx a diverticulum is given off. It passes backward under the alimentary canal to the extreme posterior end of the head, which is separated from the thorax by a thin, structureless, cuticular membrane, staining pink in hematoxylin and eosin preparations. Within this diverticulum lie the piercers and the salivary duct. The piercers (Plate LX, 7 and 8) consist of dorsal and ventral elements, and their total length is approximately 1.2 millimeters. The ventral element is made up of two parts, a dorsal and a ventral, which are very closely apposed to each other throughout the greater part of their length.

The sheath

The wall of the sheath is continuous with that of the stomodaeum and consists of somewhat flattened epithelial cells lined by a fine chitinous intima (Plate LXI, 7). On its inner surface next the coelom the sheath is also covered by a fine chitinous cuticula, the origin of which is discussed later. Its dorsal and lateral walls are of uniform thickness and appearance, while on the ventral wall there is imbedded a chitinous plate. This plate occupies approximately the posterior two-thirds of the floor of the sheath and is separated from the anterior third by a transverse suture. A similar condition has been described by Harrison (1916b:209) in the body louse. In this region of the plate there is a central groove in the

floor of the sheath. Posteriorly the diameter of the sheath decreases, until in the region of the rami of the piercers it surrounds them closely.

The piercers and the salivary duct

The piercers resemble long-handled two-pronged forks, having the prongs, which are 0.23 millimeter in length, situated posteriorly. They are long and slender, and lie free in the anterior part of the sheath, while their posterior forks are imbedded in tissue, completely filling the lumen so that sheath and piercers form a compact mass. This tissue extends forward among the piercers in two slender, pointed prolongations. A similar arrangement of tissue has been described by Sikora (1916:38) in the clothes louse. The dorsal element consists of two half tubes which in sections appear like two brackets having their contiguous edges fused (Plate LXI, 2). Posteriorly these become flattened, and after forking attain a width of 0.25 millimeter at their widest part, whence they narrow again and finally end in two ligament-like bands which come together at the point of their insertion in the posterior wall of the sheath. Anteriorly the two halves do not lie side by side, but are curved upward and toward each other so as to form a tube. The ventral aspect is made up of two parts, a dorsal and a ventral, which are closely apposed to each other but can be pulled apart without injury to either after being dissected out from the surrounding tissue. The posterior rami of the dorsal part are wider than those of the dorsal element of the piercers, and are somewhat different in shape (Plate LX, 6). They do not become flattened, and in sections appear subcircular. A small lateral process is given off from each shortly before they unite to form the piercer, which is a moderately heavily chitinized groove with more delicate edges spreading out flangelike over the edges of the ventral part of the piercer (Plate LXI, 1). The latter is also a canal-like structure (Plate LXI, 2), and its posterior rami are imbedded in the floor of the sac. Both parts of the ventral element of the piercers are bilobed at their proximal end. The lobes of the ventral half are somewhat wider apart than those of the dorsal, and both are finely serrated.

The salivary duct lies between the dorsal and ventral elements of the piercers, and at its posterior end is dilated in the form of a slender bulb which can be seen lying between the rami of the dorsal element, to the ventral surface of which the duct is attached through part of its length

by a strand of tissue. Anteriorly it appears to lie free between the elements, while just behind the haustellum it lies within the canal of the dorsal part of the ventral element. This duct was seen and figured by Stevenson (1905:13), but its function was not recognized until Harrison (1916 b:209) carried out his investigation of the mouth parts.

When the piercers leave the sheath at the junction of the buccal plate with the pumping pharynx, they bend at an obtuse angle and pass forward in the groove of the buccal plate beneath the pumping pharyngeal tube to the mouth opening (Plate LXI, 1–4).

Musculature of the mouth parts

In the region of the rami the sheath is no longer a structure distinct from its contents, and both sheath and contents are controlled by one set of protractor muscles (Plate LX, 6). These originate as slender strands in the posterior end of the sheath, where the free ends of the rami are imbedded in its wall. They pass forward along the ventro-lateral borders of the sheath and are inserted in the lateral borders of the ventral plate (Plate LX, 6). The individual strands vary in length, so that, if they be detached from their origin and pulled away from the sheath, they resemble the extended dorsal fin of a fish. The longest strands extend to the anterior border of the plate. The contraction of these muscles bends back the ventral plate and telescopes the hinder part of the sheath into the front part, so that the piercers are pushed out of the head.

The retraction of the piercers and the sheath to their resting position is brought about by two sets of retractor muscles, a lateral and a posterior. The lateral retractors consist of two muscles originating in the wall of the head and inserted in the lateral wall of the sheath in the region of the anterior border of the ventral plate. The dorsal lateral retractor originates in the dorso-lateral posterior angle of the head and passes obliquely downward and forward between the bands of the tendon muscle and the brain to its insertion in the sheath. The ventral lateral retractor is considerably shorter than the dorsal, and originates in the latero-ventral wall of the head alongside of the ventral retractor of the pharynx, whence it passes forward to its insertion in the sheath (Plate LX, 6). The posterior retractors are two large muscles lying on either side of the end of the sheath almost in the neck, two muscles lying under its ventral surface, and two lying on its dorsal surface. Each of the first has a

double origin, one branch originating in the dorsal wall of the head and the other in the chitinous cuticula between the head and the thorax. After the fusion of the two branches each muscle passes ventrad and slightly forward to the level of the floor of the sheath, where they bend at a rather sharp angle and pass a little way backward to their insertion in the floor of the sheath under the anterior ends of the rami (Plate LX, 6). The ventral muscles are two stout strands originating in the ventral wall of the neck and passing forward under the sheath almost to the angle of its posterior retractors, when they bend sharply back on themselves. Each muscle almost immediately divides into two slender strands, which are inserted in the posterior ends of the rami of the elements of the ventral piercer. They are the retractors of the ventral element of the piercers. The dorsal muscles lie on the dorso-lateral wall of the sheath and are the retractors of the dorsal element of the piercers. They originate in the posterior chitinous cuticula between the head and the thorax, and lie doubled on themselves just as do the retractors of the ventral element of the piercers. They are inserted in the posterior ends of the rami of the dorsal element of the piercers. The lateral posterior retractors control the sheath and the piercers, while the dorsal and ventral posterior retractors control the movements of the separate elements of the piercers. The contraction of the lateral retractors of the sheath brings its anterior part to a resting position, and the simultaneous contraction of the posterior retractors begins the withdrawal of the mouth parts from the wound. They come to their final resting position through the relaxation of the protractor muscles and the consequent straightening, through its own elasticity, of the plate imbedded in the floor of the sheath.

The true relationship between the pharynx and the sheath and mouth parts can be fully understood only if the study of serial sections supplement that of gross dissections and mounts *in toto*. In a section through the head at the anterior level of the attachment of the basal part of the "mandibles" of Enderlein to the lateral wall of the head, the two halves of the dorsal piercer are seen lying tubelike close under the dorsal wall of the buccal plate and are here more strongly chitinized than elsewhere. Beneath it lies the ventral element of the piercers, with the salivary duct in its canal (Plate LXI, 1). The pumping pharyngeal tube does not reach this far forward when in its resting position. From the ventral wall of the buccal plate two outgrowths are continued ventrad as a chitinous

cuticula on either side of the mouth parts, below which they pass closer to each other for a short distance before turning at right angles and passing to the lateral walls of the head. At the anterior level of the "mandibles" (Plate LXI, 2) the buccal plate is somewhat more tubelike, but it still continues ventrad as a delicate cuticula alongside the mouth parts. This prolongation appears now to be a continuation of the dorsal and ventral surfaces of the plate, while in succeeding sections it comes to be a continuation of the dorsal ends of the pumping pharyngeal tube, the anterior ends of which are now seen lying between the buccal plate and the dorsal element of the piercers. In this anterior region a band of tissue crosses the head transversely above the stomodæum and appears to be attached at either side to the lateral wall of the head just dorsad of the basal part of the "mandibles" of Enderlein. It is very similar to epithelial tissue, and each cell has a definite nucleus lying near its base. The cells attain a considerable length, particularly on either side of the stomodaeum, and their dorsal surface is attached to a well-defined basement membrane. In sections stained with iron hematoxylin they closely resemble secreting cells. At the level of the articulation of the basal part of the "mandibles" of Enderlein with the triangular part, this band of tissue rests on the top of the buccal plate, and at its most posterior part it appears to form an attachment between the buccal plate and the lateral wall of the head. The buccal plate gradually becomes flat and there is a marked increase in the thickness and rigidity of the dorsal wall of the head. Also the shape of the buccal cavity changes, marking the beginning of the ventral wall of the diverticulum, but the mouth parts are still lying under the pumping pharyngeal tube. As the chitinous intima of the buccal cavity passes dorsad, it curves around into the lateral edges of the dorsal element of the piercers, and at this point shows stronger chitinization, afterward continuing as a fine cuticula to the ventral ends of the halves of the pumping pharyngeal tube. The dorsal ends of these half tubes are also continued as a fine cuticula, which passes downward to surround the ventral part of the buccal cavity. Between these two chitinous layers is a layer of epithelial tissue which broadens considerably on either side of the mouth parts and there appears to contain some muscular elements (Plate XLI, 3). Immediately behind the section shown in Plate XLI, 3, the buccal plate divides into two arms united by a thin cuticula which forms the roof of the pumping pharynx and which, as it passes backward,

is raised in a ridge along the dorsal median line (Plate LXI, 4). The cuticular strands coming from the now more widely separated dorsal ends of the halves of the pumping pharyngeal tube are at first strongly chitinized and pass laterad to the edges of the arms of the buccal plate, where they turn ventrad and surround the sheath as a basement membrane to its epithelium. The inner cuticula of the sheath is continued upward to the ventral ends of the pumping pharyngeal tube as shown in Plate LXI, 3, but the strong chitinization in the region of the dorsal piercers extends farther dorsad, and the points passing around their lateral edges are less curved downward. The gradual movement centrad and ultimate fusion of these points cuts off the piercers from the pumping pharyngeal tube. At the same time the strong chitinization continues dorsad until it fuses with the ventral ends of the pumping pharyngeal tube, which gradually move apart. In this way the pumping pharynx is formed, which, at its anterior end, has the ventral surface much narrower than the dorsal (Plate LXI, 5). The cuticula coming from the dorsal ends of the pumping pharyngeal tube is thick and strong, and fuses with the lateral edges of the arms of the buccal plate, which are here elevated knoblike and form a firm base for the insertion of the dorsal protractor muscles (Plate LXI, 4). From their lateral edges the thin cuticular layer still extends downward to surround the epithelium of the sheath. The floor of the pumping pharynx gradually broadens and assumes a rounded shape (Plate LXI, 6). In only two areas — those of the insertion of the two large pairs of dilator muscles — is there any strong chitinization of the dorsal wall of the pumping pharynx. Just behind the anterior area and after the floor has become rounded, the pumping pharynx and the diverticulum become entirely separated from each other, and a short distance behind this separation the chitinization of the ventral wall becomes stronger and that of the lateral walls less strong (Plate LXI, 7). The dorsal wall only is capable of dilation, and in the figures is seen in a resting condition. At the level of the antennae the ventral surface narrows somewhat and a stronger chitinization is evident throughout the structure as it passes into the pharynx. Also at the level of the antennae there appears the anterior part of the plate imbedded in the floor of the sheath, which becomes chitinized and bent to form a central furrow. The circular muscle of the pharynx is well developed and surrounds the anterior part as a sphincter (Plate LXI, 8), but in no case has a transverse section of the pharynx

appeared like a cross as it is figured in the man-infesting louse by the different investigators. The tissue of the pharynx wall is in parts very much developed, but its precise histological nature has not been determined. Neither in appearance nor in staining reaction does it correspond to a simple epithelium. Where the wall of the pharynx is strongly chitinized, both the muscle and the epithelium are thin (Plate LXI, 9), but in the region between the second area of chitinization and the transition to the slender esophagus the wall is so thick that the lumen is reduced at rest almost to a slender transverse slit (Plate LXI, 1).

The salivary glands

Since the time of Landois (1864:9) it has been known that lice possess two pairs of salivary glands situated in the thorax. It was Pawlowsky (1906:199–200), however, who first described the glands opening into the piercer sheath, and his name has been given to these glands by subsequent workers. Still more recently a fourth gland, situated between the rami of the piercers, has been described.

Pawlowsky's glands are simple tubular glands lying on either side of the piercer sheath, into which they open through wide conduits at the level of the eyes (Plate LXII, 1). They have at this point a depth of 0.1 millimeter and a width of 0.05 millimeter, while their length is approximately 0.33 millimeter. They rest on the tendon of the dorsal lateral retractor muscle of the piercer sheath, and this causes an oblique indentation in their posterior ventral surface. They have a lining of epithelial cells which are not clearly defined from one another and which show the usual reactions to stains. Pawlowsky (1906:200) suggests that their secretion may serve to irritate the wound or to lubricate the piercing organs, but Harrison (1916b:217) has seen no sign of glandular activity and suggests that they are functionless. No secretion has been found in the lumina of the glands in any of the sections studied, but in a rather oblique longitudinal section there is some appearance of activity of the cells. This, however, may be due to the fact that the section is rather close to the lateral wall of the gland (Plate LXII, 2).

Between the rami of the piercers lies an unpaired gland (Plate LX, 5 and 6), which was first seen by Sikora (1916:54) in *Pediculus vestimenti* and was called by her the "Stacheldrüse." It is somewhat wedge-shaped, being broadest at the anterior end, is clothed with cylindrical

epithelium, and appears to be continuous with the posterior end of the chitinous bulb which marks the termination of the salivary duct.

The two pairs of thoracic salivary glands lie closely apposed to either side of the anterior end of the stomach, and the long, horseshoe-shaped gland is folded around the oblong-ovate gland in a characteristic manner (Plate LXII, 3). In the man-infesting pediculi the glands are described as "kidney-shaped" and "horseshoe-shaped," and their position in the thorax has been variously figured by a number of authors but the smaller one has never been shown surrounded by the larger. Ströbelt (1882, English trans. 1883:89) described the glands of *Linognathus vituli* (*Haematopinus tenuirostris*) as "elongated" and "globular," and thought that the efferent duct of the former was situated at one end of the gland and that the horseshoe appearance was due entirely to the position of the gland at rest. The length of the horseshoe-shaped gland (Plate LXII, 4) is approximately 0.66 millimeter and the width of the arms 0.33 millimeter. The length of the oblong-ovate gland (Plate LXII, 5) is 0.12 millimeter and its width 0.05 millimeter. The large cells of the epithelial lining shine through the outer membrane of the gland, and at the exit of the duct the transition from these to the small cells lining the duct can be seen even in gross specimens (Plate LXII, 6). In sections the epithelial cells are seen to be considerably larger than those of Pawlowsky's glands, and the nucleus, with its dark-staining nucleolus, lies rather toward the base of the cell. There is a distinct though small lumen within each gland. The efferent ducts of the two glands pass cephalad without uniting. In gross dissection they have been followed as far as their entrance to the head, but their union with the salivary duct lying between the dorsal and ventral elements of the piercers has not been seen. In his description of dissections prepared by Mr. Bacot, Entomologist to the Lister Institute, and the late Major Sidney Rowland, of the Royal Army Medical Corps, Martin (1913:85) says the four salivary ducts open into the base of the piercer sheath; while Harrison (1916b:209) has not succeeded in tracing definite connections between the salivary duct of the mouth parts and the ducts of the glands. Sikora (1916:56) describes the ducts as passing into the head alongside the esophagus as far as the posterior end of the sub-esophageal ganglion, where they turn back, and through a ventro-caudal bend reach the end of the piercer sheath. In *Pediculus vestimenti* she figures the two ducts of each side as uniting

in a common duct for a short distance before entering the middle of the dorsal surface of the piercer sheath by a common opening, while in *Haematopinus eurysternus* she describes them as running separately to the opening into the salivary duct of the mouth parts. Peacock (1918: 115) refers briefly to Martin, and to a dissection made by Mr. Lloyd, Chief Entomologist to N. Rhodesia, as demonstrating that the four salivary ducts open into the bulbous structure at the posterior end of the chitinous salivary tube.

Of these interpretations that of Sikora is probably the most accurate, because it alone describes an arrangement of the ducts which allows of their being drawn forward by the mouth parts during feeding without danger of their rupture.

Patton and Cragg (1913:559) describe a small collection of round cells surrounding the esophagus and constant in position, which differ from the cells of the fat body in their more glistening appearance. They distinguished no duct with certainty, though in some dissections a fine filament, which may have been a duct, was seen passing upward with the salivary duct. Müller (1915) discusses these cells in connection with the fat body, but remarks that up to that time no fat has been demonstrated in them. Harrison (1916 b:220) says that in the Siphunculata (Anoplura), groups of specialized binucleate cells, richly tracheated, lie about the ducts of the salivary glands, at the base of the esophagus. Sikora (1916: 57–58) gives a detailed account of the structure and appearance of these cells, which she calls "grosszellige Drüsen," in *Pediculus vestimenti*, and mentions their presence in the other species investigated. She considers them as quite distinct from the fat cells and suggests that they withdraw some constituent from the body fluid and store it or act on it in some way before returning it to the body fluid.

In the hog louse there is a cluster of small, subcircular cells, arranged like a pair of wings, lying above the base of the esophagus. Between these cells and the esophagus pass cephalad the dorsal vessel and the ducts of the salivary glands. On dissection each half of the cluster is found to consist, on the average, of forty small cells united by a network of very fine tracheoles. The two median posterior cells, which are somewhat larger than the others and pear-shaped, lie side by side on the end of the esophagus with their pointed ends caudad, and from each of them a slender tracheole passes to the surrounding network of the fat cells

scattered on the dorsal anterior region of the stomach wall. We have found only two nuclei in any one of these cells, while four or five may be present in each fat cell. Recently Nuttall and Keilin (1921:184) have published the results of their investigation of these cells. By the intracoelomic injection of ammonia-carmine, they have demonstrated that the cells in question have, in Pediculus, an excretory-accumulatory function, and so they have named them *peri-esophageal nephrocytes.*

THE ALIMENTARY CANAL AND ITS APPENDAGES

The stomach of the hog louse (Plate LXII, 7) is a simple tubular structure measuring approximately 1.98 millimeters in length. It consists of a wider anterior part 1.38 millimeters long with a diameter of 0.62 millimeter, and a more slender posterior part 0.6 millimeter long with a diameter of 0.2 millimeter, and extends from the region of the mesothorax to that of the sixth and seventh abdominal segments, where it bends cephalad on itself for a short distance, receiving the malpighian tubes and passing into the intestine when it again turns caudad.

The stomach of the adult hog louse differs from that of the man-infesting pediculi in two respects: its anterior end is not divided into two blind pockets, and it does not possess a "Magenscheibe." Ströbelt (1882, English trans. 1883:90) found no "Magenscheibe" in *Linognathus vituli* (*Haematopinus tenuirostris*), while Sikora (1916:62) found one in *Polyplax* (*Haematopinus*) *spinulosus* End. but not in *Haemodipsus* (*Haematopinus*) *ventricosus* End. Sikora describes as present in young specimens of *Haematopinus suis* a refractive whitish body on the dorsal surface of the abdomen, which in sections shows a structure similar to that of the "Magenscheibe" of man-infesting lice. In the present investigation no such structure has been seen, but the majority of the specimens sectioned have been mature lice, and the structure, as Sikora's work suggests, may be present only in the immature stages.

That part of the digestive tract lying in the thorax anterior to the entrance of the esophagus differs markedly in its structure from the true digestive mesenteron. That it is to be considered as a terminal enlargement of the esophagus, comparable to the crop of certain insects, is suggested by a number of facts. In gross specimens the musculature of the wall does not resemble that of the true mesenteron, because the circular fibers still lie outermost. At its distal end, just behind the entrance

of the esophagus the circular muscles become emphasized as a narrow band and the longitudinal fibers pass out from under them, forming, on the surface of the true stomach, with the underlying circular muscles an open-meshed network. A study of sections has revealed no trace of an esophageal valve, either where the slender esophagus passes into the enlarged part or where the abrupt transition to a digestive epithelium takes place, and the structure of the wall is identical in both slender and enlarged parts. A similar abrupt transition from the esophagus to the mid-intestine without the intervention of a valve or a sphincter has been described in the bedbug, by Cragg (1915:709). It consists of a delicate muscular coat and a layer of much-flattened epithelial cells lined by a fine chitinous intima. In the region of the above-mentioned circular muscle band there is an abrupt transition to the digestive part of the stomach, which is lined with a layer of secretory epithelial cells. In lice dissected some hours after feeding, the thoracic enlargement is frequently found empty; while in the anterior part of the true mesenteron there is a considerable volume of blood, and if a smear be made from the contents of such a stomach a large number of intact corpuscles are found. Also, where digestion is taking place the active epithelial cells shine through the stomach wall as light spots among the blood, a condition never seen in the wall of the anterior dilatation.

At the junction of the stomach and the intestine, four malpighian tubes are given off. They measure approximately 6.3 millimeters in length and 0.25 millimeter in diameter, and are about two and a quarter times as long as the combined length of the stomach and intestine. They first pass backward along the sides of the intestine, and then forward to the anterior end of the abdomen, where they turn again caudad terminating finally in the region of the last two abdominal segments. In structure they show no unusual features, and in no sections have secondary invaginations of their lumina been seen, such as are figured by Sikora (1916:67, Pl. III, figs. 14, 15) in *Pediculus vestimenti*.

Posterior to the malpighian tubes lies the small intestine. It has an approximate length of 0.43 millimeter and diameter of 0.2 millimeter. When empty its epithelium, which is much more slender than that of the mesenteron and is covered with a delicate intima, lies in six longitudinal folds. Three muscle layers are present, but are not readily distinguished

since the longitudinal fibers are gathered in six strands. There is no valve between the stomach and the small intestine.

Between the small and large intestines is a region, measuring 0.25 millimeter in diameter, which is characterized by the presence of six whitish, oblong-ovate plates imbedded in its wall (Plate LXII, 7). These plates, which in sections (Plate LXII, 8) are seen to extend a considerable distance into the lumen of the intestine, are surrounded by a large number of tracheae. They have no definite cell structure, their content is granular with nuclei scattered throughout, and in some sections irregular clefts are present which are evidently not due to mechanical rupture and may be definite lumina. No ducts opening into the intestine have been seen. With hematoxylin and eosin the groundwork stains an uneven pink, and with iron hematoxylin a light grayish brown. Whether these plates are modified glands is uncertain. Their inner surface is lined with a well-defined intima, and at either end a definite epithelium is represented by a few cells in the clefts between the plates, but in the middle of the region (Plate LXII, 8) no such cells are to be found. The inner layer of circular muscle is present, and the longitudinal muscle consists of six bands each made up of six or seven fibers lying in the indentations between the plates, but no outer circular layer has been seen. Sikora (1916:67–68) calls these plates the "Enddarmdrüse," and objects to the use of the name "rectal glands" on the ground that in the louse these plates have no connection with the rectum. Her figures of their structure in *Pediculus vestimenti* represent them as much more glandlike than they appear to be in *Haematopinus suis*. Toward the posterior end the cuticula increases considerably in thickness and the plates are succeeded by a well-defined epithelium. The longitudinal muscle fibers are lost sight of among the large circular fibers surrounding the rectum (Plate XLII, 9). This is a short, straight tube leading direct to the anal opening and measuring only 0.18 millimeter in length and 0.08 millimeter in diameter. Its wall lies in six folds, and it is lined by a thick cuticula which is not very strongly chitinized and stains a clear blue with Mallory's connective-tissue stain after fixation in picro-aceto-formol.

FEEDING AND DIGESTION

In experimental feeding, when a louse is placed on the arm it crawls around and appears to test the surface with the antennae and the sensitive

areas in front of the head. When the spot for feeding has been selected, the contraction of the dorsal and ventral protractor muscles, assisted perhaps by the contraction of the tendon muscles in the side of the head, moves forward the buccal plate and the pharynx, bringing the former with the inclosed pumping pharyngeal tube in contact with the skin. At the same time the haustellum is automatically pushed out, so everting the buccal teeth, which anchor the head to the skin of the host; and the sheath and piercers must also be carried forward, since the cuticula of the sheath is continuous with that of the buccal cavity. Immediately following the contraction of the protractors of the pharynx, the protractors of the sheath and the piercers contract and telescope the hinder part of the sheath into the front part, carrying with it the piercers and the salivary duct, which are inserted into the skin of the host. Salivary secretion passes into the wound, and probably contains an anti-coagulin similar to that demonstrated by Nuttall (1917c: 74) in the saliva of the man-infesting louse. The closing of the anterior sphincter of the pharynx causes a negative pressure in the pumping pharynx, the dorsal surface of which is meantime raised by the contraction of the dilator muscles, and the blood flows through the canal of the dorsal piercers to the pumping pharyngeal tube and so to the pumping pharynx. When the latter is filled with blood, the simultaneous relaxing of the interior sphincter of the pharynx and of the dilator muscles of the pumping pharynx drives the blood into the pharynx, whence it passes to the esophagus on the relaxation of the posterior sphincter. From the esophagus the blood is carried by peristalsis to the rest of the alimentary tract. The process can best be seen in newly molted specimens, and is so rapid that the muscles either act simultaneously or in very rapid succession. At the close of feeding, the whole structure is brought to its resting position by the contraction of the retractor muscles and the relaxing of the protractors, while the elasticity of the plate imbedded in the floor of its posterior region gives the final impetus to the piercers and the sheath.

The wall of the mid-intestine consists of the usual four layers, a delicate epithelium resting on a basement membrane and surrounded by inner circular and outer longitudinal muscles which are arranged in a very loose network comparable to that described by Cragg (1915:712) in the bedbug. The epithelium of the stomach is similar throughout, no definite areas being adapted respectively for secretion and absorption,

and in accordance with the mode of life of the insect it appears to be always in a state of activity. In the study of the epithelium many series of sections of the alimentary canal have been made, at intervals of from half an hour and one hour after the time of feeding up to twelve hours, by which time the stomach in captive specimens appeared to be empty of blood. Sections have also been made of lice starved to the point of death.

The epithelial cells vary in outline according to their state of activity. In the resting stage (Plate LXIII, 1) they are flattened and extend farthest into the lumen in the region of their nuclei. During absorption the individual cells expand until they appear cuboidal, and during secretion the free ends of the cells, where the ball of secretion accumulates, become subcircular. These secreting cells show great variation in the degree to which they extend into the lumen. They may remain attached to the basement membrane by a broad base, or they may be greatly attenuated and apparently attached to the membrane by a very narrow base, and in sections blood is seen extending between the individual cells (Plate LXIII, 1). In no case has a definite cell wall been found between any two cells, and the whole appearance suggests a syncytium; but further proof would be necessary before the acceptance of this view. Each cell has a large oval nucleus with a subcentral nucleolus surrounded by irregularly scattered chromatin granules. There is considerable variation in the position of the nucleus in the cell, and this, in addition to the irregularity of the cells, gives the effect of a several-layered epithelium (Plate XLIII, 1 and 2). In most cases the nucleus is seen lying in the cytoplasm immediately behind or to one side of the secretion products, and on their excretion remains intact, but in a few cases the nucleus has been seen to be carried along with the secretion (Plate LXIII, 2). In the latter case the death of the cell must follow, and the question of its replacement arises. In many insects a regular destruction of the epithelium takes place and new cells are formed from regenerative centers, or nidi; but no such structures are present in the hog louse, nor has Sikora (1916:65) found them in *Pediculus vestimenti*. Nuclear division has not been seen taking place in the epithelium, but just within the basement membrane at the base of and between some of the epithelial cells lie single, very small nuclei, each hardly more than a nucleolus, definitely surrounded by a small amount of protoplasm; and these may be the source of the new epithelial cells. A similar condition was described by Van Gehuchten

(1890:246) in the larva of *Ptychoptera contaminata*. The epithelial cells are bounded on their free edges by a border, which appears in most cases to be definitely striated.

Taken from its host and confined without food, the hog louse is a short-lived insect, and starved specimens invariably died in from twenty-eight to thirty hours after their last feeding. In lice killed, respectively, seventeen and twenty-four hours after feeding, and sectioned, the stomach was found empty of food, its walls contracted, and the majority of the cells swollen with secretion while in some cases the border of the cell was ruptured and the ball of secretion had escaped into the lumen. This would suggest that hunger stimulates the activity of the secreting cells, and also the liberation of their products into the lumen.

From a louse fed two hours previously, the stomach was dissected out in physiological salt solution and a part of the wall teased. Microscopic examination revealed the presence within the cells of two types of granules, of which the more numerous were fine, irregular-elongated, and dark, and the less numerous were coarse, round, and refractive. A 2-per-cent solution of osmic acid was then introduced under the cover glass, and the coarse granules turned black, showing them to be either lipoid or proteid, while the fine ones probably represented secreting granules. A series of twelve lice were killed with chloroform at intervals of one hour and the stomachs immediately dissected out in a mixture of equal parts of 2-per-cent osmic acid and salt solution and fixed in Flemming's weak solution for twenty-four hours. After sectioning, some were mounted unstained and others were stained with safranin. Absorption evidently began almost immediately, for at the end of one hour a few deep black granules were found just beneath the border of the cells of the anterior region of the stomach. As the series was ascended, the black granules increased greatly in number and in size. The largest lay just under the border of the cell, and their size was in inverse ratio to the degree of penetration within the cell. In the first six of the series a definite increasing absorption could be traced in the bulk of the cells lining the wide section of the stomach, and this absorption was going on even in cells forming secretion. In the latter the black granules lay in a circle outside the zone of secretion, and were never seen to come in contact with it even in the few cases in which the border had given way and the secretion was in process of being excreted. In the louse killed at seven hours, absorption was proceeding,

not in the anterior, but toward the posterior, half of the stomach, in the region of the bend cephalad; and in the last numbers of the series it was found throughout the whole slender part of the stomach.

In the cells containing the greatest number of granules, some were seen resting on the basement membrane and a few appeared to be lying among the muscle fibers outside the membrane, but sufficient evidence to prove that they had passed through the membrane unchanged is wanting. Whatever may have been the fate of these granules, they disappeared from the cells, leaving in their places numerous vacuoles among which the first traces of secretion were seen. The secretion accumulated in the form of a compact mass, resembling a ball of thread, whose surface layer takes a deep stain while the axis remains almost clear. This ball pressed against the free ental border of the cell, pushing it into the lumen and finally rupturing it.

The above experiments show that absorption and secretion are carried on by the same cells. In every section some cells, evidently in a resting stage, are seen, but it is not clear whether the cells pass through this stage after each secretion or at longer intervals. The formation of the secretion appears to begin at the close of absorption, and, as the study of the starved lice suggested, its excretion is stimulated by hunger, so that it is already present in the stomach when the blood is ingested. No attempt has been made to investigate the exact nature of the granules or the changes they may undergo, as this would necessitate a long series of experiments with various reagents, such as were carried out first by Fischer (1899) and later by Murlin (1902).

If lice be fed as in the previous experiment, and blood smears be made from the stomach contents at intervals of one hour and stained with Wright's stain, the gradual action of the epithelial secretion on the blood can be followed. Within one hour after feeding, the red cells become vacuolated and fat globules appear, but the leucocytes and the platelets are evidently not affected. The changes in the red cells continue until only an amorphous mass remains, which, in sections stained with hematoxylin and eosin, can be recognized as a mass of brownish granules. No blood platelets have been seen in any but one-hour smears. At two hours the nuclei of the leucocytes are intact but their cytoplasm has been attacked; there is a gradual change in its staining reaction, and after three hours it takes the basic stain, appears light blue, and can be distinguished

from the background only with considerable difficulty. At six hours the nuclei of the leucocytes show the first signs of disintegration, while at eight hours the whole has an amorphous appearance and the hemoglobin is disappearing.

In accordance with their parasitic habit, hog lice probably draw blood from their host at frequent intervals and in small quantities; so that in any one specimen taken at random and fixed and sectioned, all stages of digestive activity will probably be found in the length of the mid-intestine. Those fed to repletion in captivity showed absorption taking place, as it were, in a gradual succession throughout the canal; and even in these cases, not only have one or more cells in a state of active secretion been found scattered among the absorbing cells, but absorption and secretion have been seen taking place at one time in the same cell.

THE FAT BODY

In both larva and adult the hog louse is richly supplied with fat cells arranged in a more or less definite plan. In the head they lie along the lateral regions among the muscles and are most numerous toward the ventral surface. There are also two small clusters dorsad of the sub-esophageal ganglion just behind the brain. On the dorsal surface of the thorax a cluster of fat cells lies above the occipital apodeme, while on the ventral surface, between the ganglia and the hypodermis, lie four compact, grape-like clusters which extend laterad to the coxae. In the abdomen, with the exception of three clusters on the dorsal surface in the region of segments 5 and 6, the fat cells are not arranged in compact groups but are more widely spread in dorsal and ventral peripheral layers. They are more numerous among the lateral abdominal muscles than among the viscera, particularly in the female. In the male these lateral cells are crowded between the blocks of muscle and the body wall in the neighborhood of the spiracles.

In gross dissection the fat cells can be removed in clusters held together by a rich network of tracheae. They are large, subcircular cells whose wall is a transparent membrane through which the granular content is clearly seen. In sections (Plate LXII, 10) the cells are seen to contain a variable number of nuclei, each with an oblong-ovate nucleolus surrounded by a clear zone in which are scattered chromatin granules of varying

sizes, the largest being peripheral in position. Both in cells stained with hematoxylin and eosin and in those stained with iron hematoxylin, the groundwork appears to be alveolar with many dark-staining granules adhering to the walls of the alveoli. When they are stained with iron hematoxylin and the differentiation with the iron-alum solution is not carried far, it is impossible to distinguish the fat from the other granules; but if the destaining is carried further than is customary, the fat retains its black color, while the other granules become a grayish brown.

In living specimens the distribution of the fat body is clearly seen shining through the integument, and in mature specimens there may be seen in the abdomen many green cells scattered among the white fat cells. In his description of the fat body of Phthirius, Landois (1864:11) mentioned emerald green cells which stood out with greatest clearness in the lateral region of the abdomen of adult males, but he did not refer to such cells in his later work on the two species of Pediculus. Graber (1872:152) also described, in Phthirius, cells with a greenish, transparent, viscous content and usually with two distinct nuclei. In *Linognathus vituli* (*Haematopinus tenuirostris*) Ströbelt (1882, English trans. 1883:90) found that "a fine and delicate membrane envelops the yellowish green, finely granular contents, which readily allow two nuclei to be recognized," while in the abdomen he saw small, globular cells with darker-colored contents. Nuttall (1918:378) has also mentioned these green cells as appearing in Phthirius when the insect attains sexual maturity. He criticizes the statement of Oppenheim (1901) that the pigment is formed by a ferment in the salivary glands and is deposited in the insect's fat-body, and states that the significance of the pigment is yet to be determined. In sections through mature lice these cells are found lying among the fat cells in the lateral regions of the abdomen. They are much smaller than the fat cells, and have, as a rule, only one nucleus with a well-defined nucleolus, although two nuclei have sometimes been seen. Their cytoplasm is filled with granules which stain a neutral tint as compared with the positive tint taken by the granules in the fat cells. The structure and position of these green cells suggest their interpretation as oenocytes, or further investigation may prove them to be disseminated nephrocytes such as Nuttall and Keilin (1921:184) have just described in Pediculus.

THE REPRODUCTIVE ORGANS

Male

Mjöberg (1910:226-229) was the first to give an account of the male reproductive organs of *Haematopinus suis* Leach. He interpreted the male copulatory apparatus and introduced the following nomenclature for the different parts: (1) the *basal plate*, lying within the body, articulating distally with more or less free structures, the ejaculatory duct always passing dorsal to it; (2) the *parameres* (a term used first by Verhoeff in relation to Coleoptera, and quoted by Mjöberg), strongly chitinized parts articulating on the distal part of the basal plate; (3) the *preputial sac*, surrounding the penis and the distal part of the ejaculatory duct and appearing to be attached to the distal part of the basal plate between it and the parameres. Mjöberg suggested that the sac, like the penis, may have originated from an invagination of the ninth and tenth intersternital cuticula. He mentioned the mesodermal organs very briefly, giving most of his description to the ectodermal parts, which he figured with the penis both at rest and ejected.

With the exception of Ströbelt, the earlier workers dealt exclusively with the lice infesting man. Swammerdam did not describe the male reproductive organs; the forty specimens he studied were females. Leeuwenhoek (1695:387, and 1697:187 [English trans. 1807:163]) first discovered the male, but regarded the penis as a sting. Gaulke (1863) thought the penis was an ovipositor for inserting the eggs under the skin. Landois (1864:17–21 and 1865a:52–54) described and figured the male reproductive organs of *Phthirius inguinalis* and *Pediculus vestimenti*. Graber (1872:158–159) referred to the work of Landois, and dealt briefly with the structure of the seminal vesicles and the copulatory apparatus, suggesting that the latter was a much more complicated organ than Landois had thought. Ströbelt (1882, English trans. 1883:99) described the male generative organs of *Linognathus vituli* (*Haematopinus tenuirostris*) very briefly and incompletely.

More recent work on the genitalia of the lice affecting man has been done by Pawlowsky (1908), Patton and Cragg (1913), Müller (1915), and Nuttall (1917 a). The work of the last-named is the most complete account yet published of the copulatory apparatus of the Pediculidae. It does not include the internal reproductive organs. According to

Nuttall (page 304 of reference cited), " the essential parts of the apparatus are: (1) the basal plate, (2) the dilator (parameres), (3) the vesica penis [preputial sac], including its rib or strut, statumen penis, embedded in its wall, (4) the penis, and (5) the ductus ejaculatorius." In the preceding year Cummings (1916:257) had given the following explanation of the terminology used in describing the male copulatory apparatus of Siphunculata (Anoplura) and Mallophaga:

> In almost all Anoplura and Mallophaga, it is easy to recognise at once the basal plate and the parameres. The basal plate — probably double in origin as two longitudinal apodemes — is a chitinous lamina usually, if not always, longer than broad, to the posterior lateral angles of which are articulated the two chitinous appendages known as parameres. Between the parameres is the mesosome, the parts of which are not so readily made out unless a specimen be carefully dissected. Fundamentally, the mesosome is a sac — the enlarged and extrusible end continuous with the ductus ejaculatorius. This sac — called by Mjöberg " the preputial sac " — presents two regions of chitinisation — a distal and a proximal. At the distal end is the rod of the penis or virga, with frequently a splint on each side called the telomere, and one below — the hypomere.* At the proximal end are the endomeres, usually strongly chitinised bands or rods, one on each side, supporting the membrane of the sac, of which they are only local thickenings. The whole of the genitalia exhibit enormous variety in form, and the mesosomatic parts in particular are occasionally so much modified that it becomes difficult to recognise their conformation to the general plan just sketched out above. For example, in many Philopterids, such as Docophorus, no sacular portion of the apparatus is recognisable, and the distal chitinisations lie well back within the proximal, the whole forming a solid and compact mesosome. The above terms are, therefore, adopted solely for convenience of description.

* For these terms, first applied to specialised Philopterid forms, see Waterston, Annals of the S. African Museum, vol. x, pt. 9, 1914, p. 279.

In the hog louse the mesodermal reproductive organs of the male (Plate LXIV, 1) consist of two pairs of testes, slender vasa deferentia, seminal vesicles, and a long ejaculatory duct, and the ectodermal organs (Plate LXIV, 1 and 2) of a penis, a vesica penis, a basal plate, and parameres.

The testes are oblong-ovate with somewhat bluntly rounded ends, and the individuals of each pair touch at one end, where each opens into its vas deferens, which almost immediately unite to form a single canal. The testes lie on the dorsal wall of the mid-intestine between the metathorax and the posterior border of the fifth abdominal segment. Their free ends point respectively cephalad and caudad, and the left pair frequently lie a little anterior of the right. The vasa deferentia are long, very slender tubes lying coiled upon themselves and then passing backward to the region of the eighth abdominal segment, where they pass into the seminal vesicles just below the rectum. The latter are closely apposed to the wall of the mid-intestine and pass directly cephalad to

the anterior border of the fourth segment, where they turn ventrad and slightly caudad, appearing as a blunt angle on the ventral wall; again passing laterad and caudad, they turn cephalad at the posterior border of the seventh abdominal segment and cross the ventral wall parallel to the posterior arm of the above-mentioned angle, turning caudad about the anterior border of the third segment. In the region of the fourth segment they unite to form the single ejaculatory duct, which crosses the mid-intestine parallel to the last loop of the vesicles and is easily recognized by its marked musculature. Near the anterior end of the basal plate the duct loses its thick muscular wall and becomes a thin-walled muscular tube which is twice folded upon itself and then passes along the median line dorsad of the basal plate through the wall of the vesica penis into the chitinous penis.

A study of the copulatory apparatus of Haematopinus reveals a general resemblance to that of Pediculus and a much more detailed resemblance to that of the more closely related *Linognathus limnotragi* Cummings. The basal plate (Plate LVIII, 9, and Plate LXIV, 1, 2, and 3) lies within the ventral body wall and is much longer than broad, extending cephalad to the anterior border of the sixth abdominal segment. Its proximal end is rounded; it appears to consist of two halves joined along a median suture, which indicates its probable double origin, according to Cummings, as two long apodemes. Its anterior edge is weakly chitinized. Then follows a region of strong chitinization for muscle attachment, where there are two small apodemes along the median line, one dorsal and one ventral. The median chitinization soon disappears, but the lateral continues as stout borders ending in knoblike enlargements with which the parameres articulate. In cross section the plate is seen to consist of two lamellae, a dorsal and a ventral, and anteriorly these are fused along their lateral borders. In the region just anterior to the articulation of the parameres the lamellae become slightly broader and the two surfaces separate from one another. The inner, or dorsal, lamella grows up and closely surrounds the dorsal wall of the vesica penis, and on its lateral regions the parameres develop as chitinous thickenings. The outer, or ventral, lamella grows up surrounding the whole copulatory apparatus, and at its dorsal lateral borders forms a deep fold on each side for muscle insertion (Plate LXIV, 1 and 5). Such an outgrowth of the basal plate was not seen by Mjöberg,

and according to Nuttall is not present in Pediculus. Cummings (1913: 260) has described a somewhat similar condition in *Linognathus limnotragi* Cummings in which the parameres

> are of a remarkable type. Proximally they are broad blade-like pieces which meet each other (but do not fuse) beneath the mesosome in a fairly long median groove, then dorsally wrap themselves around the mesosome lying between them, forming a kind of sheath, from the end of which the penis projects, and, like the somewhat narrower distal ends of the parameres, curls up dorsalwards.

The parameres are two strongly chitinized regions on the lateral walls of the dorsal lamella of the basal plate, and articulate anteriorly with its lateral processes in the region of the seventh abdominal segment (Plate LXIV, 1, 2, 3, and 5). They are boat-shaped structures, with the keel external and lateral, and can be seen through both dorsal and ventral aspects. Distally they almost meet on the median line and proximally they diverge. The distal points appear to be less strongly chitinized than the remainder of the structure. In feeding experiments males approaching females were frequently seen to protrude and withdraw the parameres.

The vesica penis (preputial sac of Mjöberg, mesosome of Cummings), when lying within the body, rests within the upper lamella of the basal plate, its walls are thrown into folds (Plate LXIV, 1 and 3), and its anterior part is invaginated within the more posterior part. When ejected (Plate LXIV, 3 and 4) it passes backward and slightly downward for about half its length, when it bends slightly upward again. It is from one-half to three-fourths of a millimeter long and at its widest posterior part is approximately half as wide as its length. At its distal end on either side, directly on the median lateral line, are two small lobes covered with teeth, as is the whole sac with the exception of an area on the ventral surface near the proximal end. The thin, smooth wall of the sac surrounds the penis like a sheath for one-half of its length from the point of branching to the tip. It points directly dorsad. At its distal end the sac appears to be continuous with the basal plate. Above the copulatory apparatus and between it and the anal opening is the pregenital fold. No postgenital fold is present, unless the dorsal and ventral lamellae of the basal plate be considered as forming such.

The penis is a strongly chitinized tube made up of two half-tubes closely apposed to each other (Plate LXIV, 1 and 4). It lies within the vesica penis, its posterior pointed end turned toward the canal between the parameres, and its anterior part, into which the ejaculatory duct passes, in

line with their basal articulations. Here the chitinous structure is no longer a canal, but two divergent arms which may correspond to the statumen penis of Nuttall.

When killing lice with chloroform it was noticed that the males frequently ejected the copulatory apparatus in part or completely, and this characteristic has been utilized in the study of the musculature and movements of the apparatus. The protractor muscles of the basal plate have their origin in the ventral wall of the ninth abdominal segment where it turns dorsad, and their insertion in the anterior ventral surface of the basal plate. They form a thin plate of muscle fibers lying parallel to one another and identical in outline with the plate. When they contract, the basal plate is drawn caudad until the proximal edge lies just anterior to the boundary between segments 6 and 7, and the parameres are protruded from the sexual orifice for from one-third to one-half their length. Their dorsal aspect shows no collar-like membrane forming a sheath for the transit of the vesica penis as figured by Nuttall in Pediculus. Its place is taken by the already described upgrowth of the basal plate. They point dorsad and slightly cephalad, so that their ventral aspect is now caudad (Plate LXIV, 4). They are controlled by muscles which lie at rest alongside them and which, by their contraction along with or immediately following that of the muscles of the basal plate, hold them rigid during copulation. There are ten muscle strands on either side, of which the five posterior lie in a regular succession and the five anterior in a close group. They originate in the ventral body wall in the region of segments 6, 7, and 8. The posterior strands are inserted in the deep lateral fold of the upgrown ventral lamella of the basal plate (Plate LXIV, 5), and the anterior strands are inserted as a stout tendon in the anterior dorsal border of this upgrowth. Mjöberg (1910:189) has explained the purpose of the genital plate, at any rate in some cases, as the basis of attachment of these muscles, and his figure of *Haematopinus bufali* de Geer shows them inserted in the border of the genital plate. Cross sections through this region in the hog louse show these muscles originating laterad of the genital plate. The dorso-ventral lateral muscles of the abdomen next contract and drive the coelomic fluid caudad and into the vesica penis, which is thereby everted carrying the ejaculatory duct and the penis along with it. The thick muscular part of the duct has been drawn caudad until its posterior end lies at the level of the articulation of the

basal plate and parameres, and the slender part has passed along the center of the vesica, where it is surrounded by a sheath composed of slender muscle fibers. This sheath originates as two lateral bundles on the proximal border of the basal plate and is inserted as fine strands on the wall of the vesica at its junction with the penis.

At the close of copulation the protractor muscles and the body muscles relax, and the coelomic fluid passes back into the body. The vesica penis is drawn to its resting position by the contraction of the muscle sheath of the slender part of the ejaculatory duct, as well as by the contraction of many fine muscle fibers which are inserted on the surface of its anterior half and have their origin in the dorsal anterior border of the basal plate. When at rest these muscle fibers form a thick layer on the anterior region of the basal plate and a thin layer between the vesica penis and the basal plate. Some muscle fibers originate in the ventral body wall between segments 6 and 7 and are inserted in the anterior border of the basal plate, and these by their contraction bring the framework of the apparatus to its resting position.

The histological structure of the mesodermal organs shows some interesting features. The testes are surrounded by a three-layered wall — an inner slender epithelium, a very fine basement membrane, and a peritoneal wall in which there is no pigment. Fat bodies are closely apposed to the dorsal surface of the testes, and among them, as also in the peritoneal wall, tracheoles are very numerous. The contents of the testes consist of cells and developed spermatozoa, which for the most part lie in clusters of from six to twelve individuals. This is similar to the finding of Landois (1865 a:53) in Pediculus, and is common in insects. Each spermatozoon has a rod-shaped nucleus in the head, which takes the hematoxylin stain so intensely as to appear black. Anterior to the nucleus can be distinguished a small area of cytoplasm staining a bright pink with eosin just as the tail stains. No middle piece can be distinguished. These clusters of spermatozoa are in that half of each testis which lies next to the vas deferens, and appear to rest in a matrix of nutritive cells with very pale-staining nuclei. The remainder of each testis is filled with cells typical of the different zones of development. At the base there is a very small cluster of spermatogonia, followed by spermatocytes of both orders in process of division and reduction, and then a small section of spermatids.

The remaining mesodermal structures are slender tubes varying in diameter. Seen in cross section (Plate LXIII, 3) the inner layer of their wall is composed of epithelial cells resting on an exceedingly fine basement membrane. Outside this is a thin, structureless layer, the true nature of which has not been determined. The anterior half of the ejaculatory duct is surrounded by a strong wall of circular muscle fibers, among which are also, toward the posterior end, strands arising at right angles to the duct wall and passing to the outer edge of the circular fibers. Nuttall (1917 a:307) attributes this strong development of muscle to the force necessary to drive the spermatic fluid down the long, slender part of the duct.

The epithelial cells lining the vasa deferentia are small and somewhat flattened, and have a straight surface in the lumen. The anterior sections of the seminal vesicles act as a reservoir for the developed spermatozoa, and there, as in the sections of the vasa deferentia, they can be seen. The epithelium of the region is regular and columnar, and the nuclei, which are circular and have a well-defined nucleolus, lie near the base of the cells, of which the cytoplasm contains many dark-staining granules. Lower in the tubes the cells lose their clearly defined inner borders and appear finely granular, while a secretion which stains a deep pink with eosin surrounds the spermatozoa. This secretion soon takes a definite form and is oval in outline, and, in appearance, not unlike a cross section of an orange or the illustration of the " Magenscheibe " given by Landois (1865a:Pl. IV, fig. 8), and it contains minute vacuoles (Plate LXIV, 6). These suggest spermatophores, but in section no spermatozoa could be seen within them. Still farther along in the vesicles the inner borders of the cells project into the lumina as blunt, thumblike processes, which are slightly pink in sections stained with hematoxylin and eosin, while the remainder of the cell is dark blue. No cell walls are seen and the cells are evidently in active secretion. The clearly defined " spermatophores " now become markedly vacuolated and gradually lose all semblance of a definite form. Probably this secretion acts as a solvent. In the anterior part of the muscular section of the ejaculatory duct the cells are small, but in the posterior part the epithelium is much thickened and has a markedly glandular appearance. From many of the cells of the vesicles and the ejaculatory duct, slender processes project into the canals and even directly into the central mass of secretion, while in some parts of

the duct they interlace, giving the appearance of a network near the epithelium. The slender part of the ejaculatory duct has a small, round-celled epithelium, but in one quarter of the wall it is thickened and projects into the lumen as a more or less blunt cone, which, in the passing of the duct to the penis, forms its dorsal wall.

In gross dissection of the parts no accessory glands have been found. Patton and Cragg (1913:559) describe and figure small glands in *Pediculus vestimenti* at the junction of the vasa deferentia with the seminal vesicles, but such are not present in Haematopinus. Nuttall (1917 a:308) mentions the accessory glands of Pediculus as lying on the muscle of the dorsal surface of the basal plate and undergoing passive movement along with the ejaculatory duct and the penis at the extrusion of the copulatory apparatus, but no such glands have been found in Haematopinus. It may be that the place of accessory glands has been taken by the enlarged glandular epithelium of the different parts of the ejaculatory duct.

Female

From the work of Landois (1864:14 and 1865 a:48) it has long been known that the Pediculidae possess polytrophic egg tubes. Graber (1872:159) differed from Landois in his conception of the egg tubes, and described them as telotrophic like those of the Hemiptera but gave no figures, and subsequent work has shown him to be wrong. Ströbelt (1882, English trans. 1883:94) made the earliest reference to the ovaries of *Haematopinus suis*, and he described them as bilocular. His findings in regard to the structure of the tubes and the development of the eggs confirmed the work of Landois. The classic work on the ovaries of Siphunculata (Anoplura) and Mallophaga is that of Gross (1906:347) in which he showed the close resemblance between the two groups. He studied four species, of which *Haematopinus suis* was one, and described in detail the gross anatomy and histological structure of the ovaries and the development of the egg. Mjöberg (1910:253) cited the work of Gross but did not himself mention the female reproductive organs of the hog louse. The female reproductive organs of the Pediculidae affecting man have been described by Pawlowsky (1908), who illustrated his work with transverse and longitudinal sections (Pl. II and III, figs. 4–12, of reference cited) but included no drawing of the gross anatomy; by Patton and Cragg (1913:560), who figured and briefly described the

organ; by Müller (1915), who also showed a number of figures; and by Peacock (1916). Nuttall (1917 a:312) described the copulatory apparatus.

The essential reproductive organs of the female are the paired ovaries and their oviducts, with the colleterial glands. The remaining parts are the uterus and the vagina (Plate LXV, 1). In the hog louse neither spermatheca nor bursa copulatrix is present.

The ovaries are clustered, consisting of five egg tubes on each side, and this number seems to be constant in the Siphunculata according to the different workers in the group, but the number of egg chambers in each tube differs in the various species. Each egg tube consists of a terminal filament, a terminal chamber or germarium, and as a rule two egg chambers or vitellaria although three are sometimes seen. The fine terminal filaments of each ovary of a pair unite, and pass as a single filament above the mid-intestine into the fat cells and their tracheoles. Graber (1872:159) alone, among the earlier workers, thought that three terminal filaments, or vessels as they were then called, passed from each egg tube; but, as Gross (1906:350) suggests, he probably confused tracheae with terminal threads. The ovaries lie in the abdominal cavity on each side of the mid-intestine, and in the region of the sixth abdominal segment they fuse to form a short common oviduct on either side. They pass into the uterus at the anterior border of the seventh segment after receiving the colleterial glands, which are large, trilobed glands with convoluted edges. Their anterior lobes, pointing cephalad, lie along each side of the mid-intestine under the lateral borders of the ventral abdominal muscle plate, and extend to midway between the posterior and anterior borders of segment 4; the posterior lobes are shorter, and, pointing caudad, extend just within the anterior border of the eighth segment; the lateral lobes surround the oviducts and the mid-intestine near the anterior border of segment 7.

The uterus is surrounded by a stout muscular wall which, as Landois (1865 a:51) first pointed out, is made up of circular as well as longitudinal fibers. After receiving the oviducts it passes caudad through segment 7 into segment 8, then bends back along itself just into segment 7, where it again turns caudad describing a semicircle, so that the point of its passage into the short, thin-walled vagina lies on its own spiral. The meaning of its length and musculature is revealed in examining specimens having a mature egg in the uterus. It is then a long, straight, and wide tube,

whose anterior border lies approximately on the anterior border of the fourth segment.

The structure of the female copulatory apparatus is much simpler than that of the male. It is situated in the last three segments of the body, and the external indications of sex are the shape of the abdomen, two triangular chitinous plates on the dorsal surface of segment 9 (which ends in two pointed lobes), and the gonopods on the ventral surface of segment 8. The gonopods (Plate LVIII, 11) are flat processes, triangular in shape. Their median free border is somewhat strongly chitinized and is set with a row of stout hairs. Anteriorly they are joined by a fold of the integument which projects caudad in two blunt points. As has already been said, they appear to have arisen as an infolding of the integument of the segment. The sexual orifice is on segment 8 under the anterior border of the gonopods. It leads directly into the vagina, a thin-walled chitinous sac lying close to the ventral body wall and at its anterior end passing into the uterus ventrad of its semicircular coil. In Pediculus the walls of the vagina are covered with minute, outward-pointing teeth. In Haematopinus no teeth could be seen on the vaginal wall in gross preparations treated with potash and mounted in balsam.

A plate of closely set muscle fibers originates in the anterior border of segment 7 immediately posterior to the ventral abdominal muscle plate, and is inserted in the anterior border of the gonopods. The contraction of these muscles raises the gonopods and brings the sexual orifice and the vagina into position for copulation. Muscle fibers originating in the lateral wall of the vagina and in that of the uterus near its passage into the vagina, are inserted in the sternite of segment 9, and by their contraction draw the vagina and the uterus to their resting position.

The histological structure of the ovarian tubes at different stages of development has been thoroughly studied and described by Gross (1906: 352–364), and a brief résumé of his work is here inserted. There is no peritoneal wall surrounding the egg tubes, and the tunica propria (basement membrane) is unusually well developed. In the terminal threads of adult females the content consists of a homogeneous granular protoplasm which Gross regards as degenerated remains of the cells to be found in younger stages. Landois (1864:16) had seen these cells also in the terminal chamber of Phthirius, and he considered them as specific yolk-forming elements and hence the terminal chamber of the one-egg tube

as a true yolk chamber. This chamber remains small, there is no boundary between it and the terminal thread, and its epithelium is composed of small nuclei between which cell boundaries are seldom seen. In young individuals the chamber contains only a few cells besides the epithelial nuclei (Plate LXVI, 4), while in older animals the cells are quite degenerated and are broken up into scattered fragments until finally only epithelial nuclei remain and these have migrated into the interior of the chamber (Plate LXVI, 7). In every case Gross found a zone of transversely arranged epithelial cells behind the terminal chamber. Such a zone is characteristic of telotrophic egg tubes and has not been found in any other group having polytrophic egg tubes. In Haematopinus it is very short and in some cases is represented only by a row of much degenerated epithelial nuclei, distributed in the longitudinal direction of the egg tube. In the egg chamber (Plate LXVI, 9) there is a definite number and arrangement of nutritive cells. There are five of these, and the odd one lies in the apex, with the others in two successive rows immediately behind. The nuclei of all are irregular in outline. Such an arrangement was seen by Landois (1865 a:48) in Pediculus. The two hindmost nutritive cells push into the plasma of the egg, and there is seen a layer of dark-stained, ball-like, little nuclei which are the nutritive substance introduced from the cell to the egg for the formation of the yolk. In the older individuals the follicle epithelium is clearly seen to be of two kinds. That surrounding the nutritive cells is thin and flat, having few nuclei and no distinct cell walls; while that surrounding the egg chamber is made up of deep cylindrical cells closely apposed on one another and containing cylindrical nuclei with an elongated nucleolus. The mitosis seen in the epithelium of younger stages has now given place to amitosis, and finally each cell contains two nuclei which lie behind each other in the longitudinal axis of the cell (Plate LXVI, 10). Gross has never seen cell division following the amitotic division of the nuclei, and in the light of more recent researches this nuclear division is to be regarded rather as a redistribution of nuclear material than as a true amitosis. Behind the egg cell the follicle cells are hemmed in by a collection of dark nuclei similar to those behind the nutritive cells, and cell boundaries are wanting at this point; both these facts support the view that in Haematopinus, as in so many other cases, the follicle epithelium cooperates in the formation of the yolk. The

successive egg chambers are connected by short stalks of epithelial cells, apparently a continuation of the follicular epithelium.

The egg tubes of each side pass into a short oviduct which receives the wide conduit of the colleterial gland before passing into the uterus. The wall of the oviduct is made up of a thin muscular layer, a fine basement membrane, and small epithelial cells with an inner delicate chitinous lining; that of the colleterial gland consists of a peritoneal membrane, a thin basement membrane, and large columnar epithelial cells with large nuclei (Plate LXV, 2). These large epithelial cells secrete the cement which glues the eggs to the bristles, and in sections stained with hematoxylin and eosin the secretion is seen as a pink, homogeneous, more or less vacuolated mass, while with iron hematoxylin it appears dark brown or black. The uterus receives the oviducts laterally and somewhat posterior to its apex. In this region the muscular coat is only moderately developed, the epithelium and its basement membrane are clearly seen, and the chitinous lining is smooth (Plate LXV, 3). Posterior to the point of entrance of the oviducts the wall is thrown into deep folds and the muscular outer coat is very highly developed. The epithelial cells are small and no distinct cell boundaries are seen. The chitinous lining is thrown into innumerable sharp convolutions resembling moderately long, sharp teeth (Plate LXV, 4), which, posteriorly in the region of the coil, appear as blunt, rather flattened teeth (Plate LXV, 5 and 6). From sections made through a uterus containing an egg, it appears that these teethlike projections retain their form when the uterus is fully expanded.

The earliest description of the egg of the hog louse is that of Leuckart (1855:140–141). He recognized the presence of a third chorionic layer, but without sections it was impossible to get a true conception of the structure. He figured a piece of the shell, showing it to be provided with innumerable canals running perpendicular to the surface of the chorion. Ströbelt (1882, English trans. 1883:96–97) described briefly the egg of *Linognathus vituli* (*Haematopinus tenuirostris*), citing Leuckart and Landois. The most complete and accurate description is that of Gross (1906:364–377), who found, in the eggs of Siphunculata (Anoplura) and Mallophaga, structures so similar as to indicate close relationship between the two groups. Mjöberg (1910:257–262) refers to the work of Gross and describes briefly the eggs of several additional species of Siphunculata (Anoplura) and Mallophaga.

The follicle epithelium of the egg chamber secretes first the vitelline membrane, which in this case is also the cell membrane of the egg, and then the chorion. According to Gross, of whose work the following is a résumé, the formation of the chorion begins at the posterior end and a thin endochorion and a thicker exochorion are formed. The former appears striated in section and may be porous. The follicle cells are somewhat convex on their inner surface and an imprint of this is left on the exochorion. Up to this time their nuclei have been lying toward their inner surface, and the formation of the epichorion (exochorion of Leuckart) begins as a constriction between the nuclei, and in the indentations so formed appear small, rather regularly rhomboid, chitinous structures. (The egg shell is not formed of true chitin, since it is soluble in potassium hydroxide.) By further constriction of the epithelial cells between the nuclei a system of hollow cavities in communication surrounds the egg, and these become almost filled by a deposition of chitin forming a distinct chitinous lamella (Plate LXVI, 21 and 22). Up to this point a nucleus has rested on each side of the constriction, but now the one between the epi- and exochorions passes through the canal leaving only a tip of protoplasm (Plate LXVI, 23 and 24). The epichorion now moves closer to the eggshell proper, and the pores assume the appearance of rather long canals (Plate LXVI, 25, a); so that looked at from the surface (Plate LXVI, 26), the epichorion appears pierced by numerous canals perpendicular to its surface (Leuckart, 1855:140; stomata of Stevenson, 1905:16). Between these pores is a network of three-sided cavities. During this development the staining properties of the epithelium have undergone a change; the protoplasm takes a deep stain, while the nucleoplasm has become transparent and the nucleolus no longer shows great affinity for stain.

On the operculum there is no epichorion formed and the exochorion is much thickened (Plate LXVI, 25, b). The chitin formation extends down the sides of the epithelial cells, but it is an outgrowth from the exochorion and not a separate formation. There are polygonal areas on the lid surrounded by a network whose ridges are much deeper than those on the egg, but, as there is no epichorion here, the two parts do not differ in level.

The epithelial cells now rapidly degenerate, and characteristic, very darkly stained structures, like broken circles, are seen in their protoplasm. On the operculum these are attached to the ridges and extend lengthwise

so that a fork is formed, between the prongs of which are transverse ridges (Plate LXVI, 28). These structures have no very regular character, and Gross could not determine whether they originated as separate rings or as lamellae. In the vicinity of the furrow between the egg and the operculum the appearance is distinctly modified (Plate LXVI, 27, b). Here the branches of the network are themselves forked and their prongs are extended as longitudinal rings; also, the transverse rings are more numerous and irregular. Behind the operculum there is still another structure. Over the network of the exochorion, and at first without any connection with it, is formed a characteristic trellis of longitudinal and transverse rings, having as a groundwork a narrow, undulating band whose curved edges lie always on a furrow of the epichorion. The whole is then set through with transverse parallel rings, some of which are found also between the epichorion network. Directly behind the opercular furrow the chorion extends as two specially large projections which bend forward and are forked at their outer ends (Plate XLVI, 27, a). These are two lamellae, which extend around the whole circumference of the egg, overarching the furrow and protecting it. In the fully developed egg (Plate LXVI, 29) the rings are said to be made of chitin and to have become a part of the chorion. The remainder of the epithelium is now an amorphous mass and is the so-called egg-white layer around the egg, of which Gross says (page 370 of reference cited): "Auch dieser Umstand, dass der Follikel schliesslich sich zur Eiweisshülle umbildet, ist, soviel ich weiss, ohne Analogon unter den Insecten." The epichorion is connected with the exochorion anteriorly at the opercular ridge and posteriorly at the egg stigma, a complicated structure whose significance is not clear. A diffusion of air through the pores cannot take place because of the egg white. An interchange of gas cannot take place, although the space between the exochorion and the epichorion contains a quantity of gas; rather is this chamber of gas to be regarded as a warm covering for the egg, or it may serve as a protection against injury from blows to which eggs attached to the hair of animals are exposed.

In the egg of the hog louse the micropyles are not indicated by any special formation. In sections they can be seen as simple canals, narrowing somewhat at their inner ends, in the vicinity of the operculum. Leuckart (1855:141) did not state their number; according to Gross (1906:371) there are at least thirty.

At the posterior pole of the egg is a very characteristic structure (Plate LXVI, 34), to which Graber (1872:165) gave the name "Eistigma." The earliest description of this structure is that of Leuckart (1855:139, 141), who observed it on the eggs of *Pediculus capitis* and *Haematopinus suis*, and it was seen also by Landois (1864:15) on the egg of Phthirius. Gross (1906:372) has given the first detailed description of it and figured its structure. The egg stigma forms a roundish swelling on the chorion and is pierced by numerous thin-walled canals, which narrow toward their inner ends and converge to one side. Gross studied its formation in detail, and in young stages found the egg follicle closed by a plug extending far into the interior of the yolk, but as growth proceeds the plug becomes leveled. The nuclei are small and the inner ends of the cells are drawn to a point. These inner ends are cut off from the cells in a characteristic manner and the nucleus is drawn to the outer wall, while between them is a zone of protoplasm in which cell boundaries can no longer be recognized. Between the detached inner pieces begins the deposition of chitinous substance, and this appears as fine striae, while at the exterior, where the deposition has become more advanced, the thin, chitinous lamellae have lost their color. Then are formed in the region of the stigma the endochorion and the exochorion. The stigma is now completely developed. The point formed by the pointed ends of the cells still remains attached inside, cell walls can be recognized, and it can be seen that each cell forms a canal.

No satisfactory biological interpretation has been found for the egg stigma, a structure found in no other insect order. Earlier authors advanced three views, none of which has proved satisfactory. Leuckart (1855:139) and Melnikow (1869:154) regarded it as an attachment disk; but if this were its function, why should it be pierced by canals in most cases? Kramer (1869:462) regarded it as the true micropyle; but in some species, for example Nirmus, the canals do not pass to the inner ends of the cells. Graber (1872:163) interpreted it as a means of aeration for the eggs and so named it; but in most cases it is covered over by secretion. The closing of the pores by secretion would be essential in Pediculus, since, according to Sikora (1915:530) and Nuttall (1917 d:148), the embryo escapes from the egg by pumping air through its alimentary canal in order to increase the pressure in the egg and force open the operculum.

TECHNIQUE

In the laboratory the following methods of keeping lice have been tried:

Conditions	Temperature	Opportunities of feeding in 24 hours	Length of life
On laboratory table in petri dishes	Room temperature	4	7–10 days
In incubator in open vials	36°–37° C., dry heat	4	Under 24 hours
In incubator in vials having in the bottom a layer of moist cotton batting $\frac{1}{4}$–$\frac{1}{2}$ inch thick	36°–37° C., moist heat	4	3 days
In a gauze bag worn on the body	35° C.±	Constant	Lice would not feed through gauze
In vials plugged with cotton and gauze and carried close to the body day and night	35° C.±	3–4	Up to 35 days
As in last experiment	35° C.±	First day, 3; second to fifteenth day, 2; sixteenth to twenty-sixth day, 1	26 days

We have found the last method the best for rearing hog lice in captivity. In the glass containers, hog bristles and teased gauze were provided as a foothold.

Chloroform has been found the most satisfactory medium for killing lice both for dissection *in toto* and for sectioning. For the former purpose, the lice may be preserved indefinitely in 80- to 85-per-cent alcohol, but the following fluid has been found much more satisfactory:

Distilled water	30 parts
Alcohol, 96-per cent	15 parts
Formaldehyde	6 parts
Glacial acetic acid	4 parts

This fluid was first used by Pampel (1914:298) in his work on the female Ichneumonidae, and he found that it kept the tissue soft and elastic for dissecting purposes. After chloroforming, a small slit was cut in the side of the abdomen to allow the preserving fluid to penetrate more rapidly.

Owing to the toughness of the cuticula, dissections could not be made on slides, and so the lice were fixed to the top of a thin layer of paraffin in the bottom of a watch glass and covered with physiological salt solution. Scalpels with curved blades, microscope scissors, and fine needles were used, and all dissections were made under a Zeiss binocular. After some practice the different systems could be removed intact and placed on slides in a drop of salt solution, where the parts could be arranged in the desired way and fixed in position with Bless' fluid according to the method followed by Patton and Cragg (1913:718-720). The material could then be carried through the alcohols and stained *in toto*. The best result in such staining has been obtained with Grenacher's borax carmine, the stain being allowed to act for from twenty-four to forty-eight hours. In dissecting organs for sectioning, the physiological salt solution was replaced by the medium in which the tissue was fixed.

In the study of the epithelium of the digestive tract, the alimentary tract was dissected out and prepared for imbedding in paraffin. In order to cut more than one stomach at a time, the method learned by Minchin from fellow workers in the Zoological Station at Naples in 1891, and used by Minchin and Thomson (1915:508) for sectioning the stomachs of fleas in their study of the rat trypanosome, was tried. Their method consisted of cutting thin free-hand sections of amyloid liver, arranging three stomachs on it with the anterior borders level, and fixing them in position with a drop of albumen fixative. This block could be oriented easily, but it was found more satisfactory to simply imbed single alimentary tracts.

In sectioning whole lice it was necessary to double-imbed in celloidin and paraffin, and three methods were followed, all of which gave equally good results. The slow method of celloidin imbedding, beginning with a thin solution and gradually increasing the thickness until the object was sufficiently permeated with celloidin to be hardened in chloroform and carried on to paraffin in the usual way, was first tried. Then, in order to shorten the period of infiltration, a modification of Gilson's rapid method (Lee, 1905:131) was substituted. At the same time the oil-

mixture method introduced by Apáthy (1912:464, 468; also Kornhauser, 1916) was used, but it gave no better results than Gilson's rapid method and involved many more steps. After double-imbedding it was found possible to make good series of longitudinal and transverse sections of 5 microns, $7\frac{1}{2}$ microns, and 10 microns, in thickness.

The reagents used for fixing were Zenker's fluid, Bouin's fluid, and Flemming's weak solution. In every case the insect was chloroformed and its legs were cut off close to the thorax before it was placed in the reagent. Both the Zenker-fixed and the Bouin-fixed material were stained with hematoxylin and eosin, hematoxylin and orange G, and methylene blue and eosin. In addition the Bouin-fixed material was stained with Mallory's anilin-blue connective-tissue stain, a combination used by Kingery (1916: 292) in studying the intestine of the grasshopper. This stain differentiates the chitinized from the non-chitinized cuticula, the former staining red and the latter a clear blue, and also brings out strikingly the striations of the muscle fibers. The Flemming-fixed material was stained with iron hematoxylin according to the method of Heidenhain, and with safranin, a solution made of equal volumes of a water-soluble and an alcohol-soluble stain being used.

All measurements given in the text were made with an ocular micrometer valued in terms of a stage micrometer used in a Zeiss microscope fitted with an objective A, 15 millimeters, and an ocular No. 2, and having a tube length of 160 millimeters.

SUMMARY

At the close of his paper on the mouth parts of the body louse, Harrison (1916 b:218) has pointed out the many resemblances found by himself and other workers between the Siphunculata (Anoplura) and the Mallophaga, particularly those of the suborder Ischnocera. The present study has served to again emphasize the general similarity in structure of the two groups, and has brought to light some structures which have not yet been described in this order.

No mention of the apodemes extending from the dorsal to the ventral surface of the thorax has been found in the literature. While the name suggested for them — the apodemes of the prothorax and the prosternum — is intended to call attention to their position in the anterior part of the thorax, it must not be forgotten that they probably originated as invagi-

nations respectively of the transverse conjunctivae between the pro- and the mesothorax and between the pro- and the mesosternum.

A second structure hitherto undescribed in the Siphunculata is found in the head, under the posterior lobes of the brain. The position and structure of this pair of bilaterally symmetrical circular bodies suggests their interpretation as the "corpora allata" of Heymons and other investigators (cited by Berlese, 1909:588, and by Schröder, 1912–13:86).

In the study of the stomodaeum and the mouth parts, the aim has been to present as accurate a picture as possible of their anatomical structure, musculature, and working. Their homology is not touched upon, because in the case of structures so far modified from the generalized type, interpretation should rest upon an investigation begun with the earliest appearance of segmentation in the embryo and continued to maturity. Cholodkovsky (1903:120) alone has touched upon this aspect, in his work on the man-infesting pediculi, whose pharynx and mouth parts are similar in plan to those of the hog louse. In none of the sections of the alimentary canal have protozoan parasites been found, and the physiology of digestion has been touched upon but briefly.

The reproductive systems and the secondary sexual characters resemble those of other members of the order, but in the female no receptaculum entering the uterus has been found. According to Harrison (1916 b:221), "in the Ischnocera, and in all Anoplura save Pediculus, a receptaculum of remarkable structure opens into this uterus by a long narrow duct, the entry of the duct into the receptaculum being marked by a conspicuous chitinous ring."

The experimental work on the biology of the species has been carried out with much care. In the acceptance of the resulting figures indicating periods in the life history, however, it must be borne in mind that in the natural habitat, with continual opportunity of feeding, these periods may be somewhat shorter.

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Plate LVIII

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Claws of adult (a, protrusible pad; b, joint between tibia and tarsus); 2, eggs attached to hog bristle (a, cap, or operculum; b, vitelline membrane; c, cement); 3, first instar; 4, second instar; 5, third instar; 6, sternal plate; 7, exuvia attached to bristle; 8, adult male; 9, ventral aspect of posterior segments of abdomen of male; 10, adult female; 11, ventral aspect of posterior segments of abdomen of female (a, gonopods); 12, apodeme of prosternum and prothorax attached to sternal plate

(3, 4, and 5 drawn from exuviae, to same scale as 8 and 10)

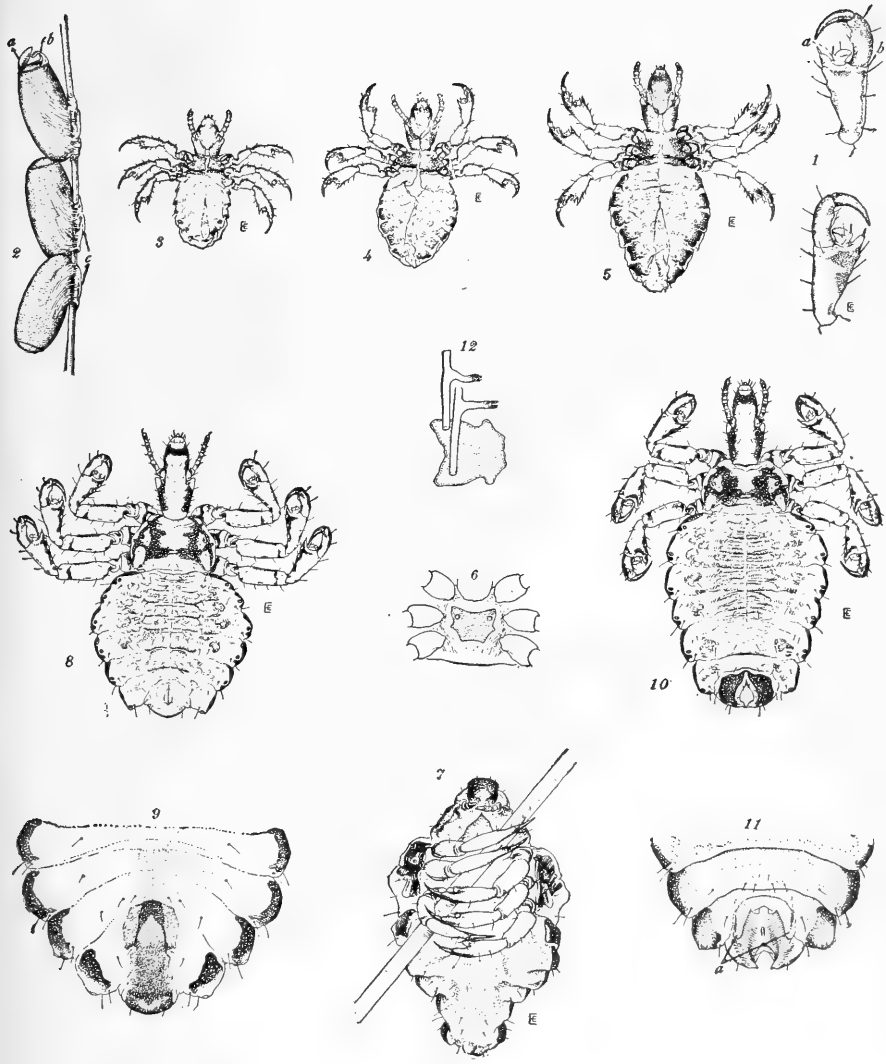
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Plate LIX

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Diagrammatic representation of primary and secondary tracheae; 2, stigma, vestibule, bulla, and trachea, drawn from cleared specimen; 3, section through abdominal stigma (a, vestibule; b, lever; c, bulla; d, intrinsic muscle; e, extrinsic muscle); 4, ventral abdominal muscle plate of female, ventral aspect; 5, right lateral abdominal muscles of segment 4 of male (drawn from gross dissection); 6, heart and one-half of length of aorta (a, pericardial cells); 7, transverse section through heart in region of ostium; 8, central nervous system and anterior part of sympathetic system (a, frontal ganglion; b, recurrent nerve; c, brain; d, subesophageal ganglion; e, connectives; f, prothoracic ganglion; g, mesothoracic ganglion; h, metathoracic ganglion and abdominal ganglion; i, visceral nerves); 9, sections through tip of antenna showing multinuclear sensory cells (drawn with oil immersion)

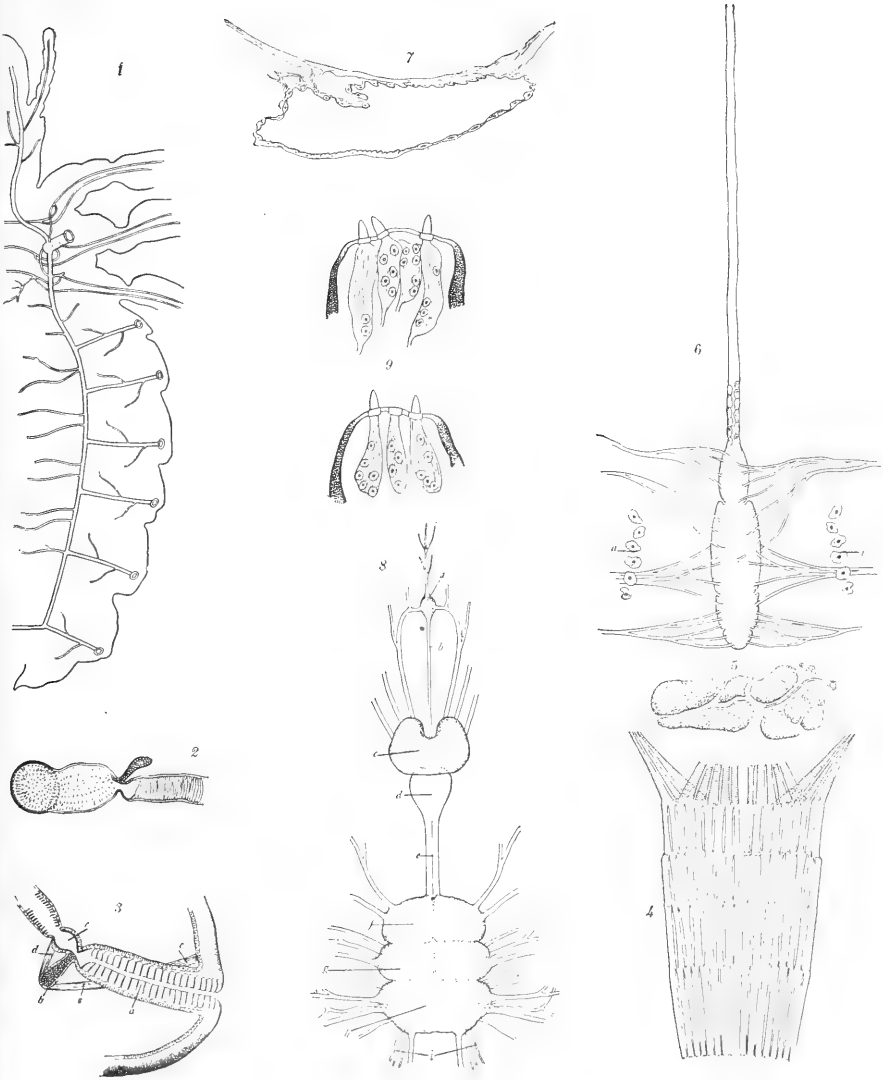
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Plate LX

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Transverse section through anterior region of head just posterior to section shown in Plate LXI, 1 (a, buccal plate; b, dorsal element of piercers; e, anterior ends of pumping pharyngeal tube; l, structures corresponding to " mandibles " of Sikora; mm, muscles of these; nn, dorsal protractors of buccal plate; o, prefrontal ganglion); 2, dorsal aspect of anterior part of stomodaeum (a, buccal plate; e, pumping pharyngeal tube; g, pumping pharynx; k, pharynx; nn, dorsal protractor muscles; pp, ventral protractor muscles; qq, anterior dorsal retractor muscles; rr, posterior dorsal retractor muscles; ss, dorsal muscles of pharynx; t, esophagus; uu, " mandibles " of Enderlein; vv, lateral tendon muscles; w, haustellum with buccal teeth; dilator muscles of pumping pharynx not shown); 3, ventral aspect of anterior part of stomodaeum (xx, ventral retractor muscles; other lettering as in 2); 4, ventral aspect of haustellum protruded and showing buccal teeth; 5, transverse section through anterior region of thorax, showing posterior ends of rami of piercers with their muscle attachments (a, cuticula enclosing piercers and esophagus; b, dorsal element of piercers; d, ventral element of piercers; ee, occipital apodeme; i, aorta; k, recurrent nerve; ll, tracheae; m, connectives; nn, posterior arms of apodemes of prothorax and prosternum; o, salivary gland between rami of piercers; t, esophagus); 6, mouth parts (b, dorsal element of piercers; c, salivary duct; dd, rami of ventral element of piercers; o, salivary gland between rami of piercers; p, anterior end of chitinous plate imbedded in floor of sheath; ee, protractor muscles of sheath and piercers; ll, ventral lateral retractors of sheath and piercers; mm, dorsal lateral retractors of sheath and piercers; nn, posterior retractors of sheath and piercers; posterior retractors inserted in end of each ramus not shown; sheath torn away leaving only ventral plate and piercers, so that lateral retractor muscles appear in approximate position); 7, dorsal element of piercers (a, bulb at end of salivary duct; salivary duct underlying piercer shown as a dotted line in proximal part only); 8, ventral element of piercers (p, chitinous plate imbedded in floor of sheath); 9, anterior ends of ventral elements of piercers

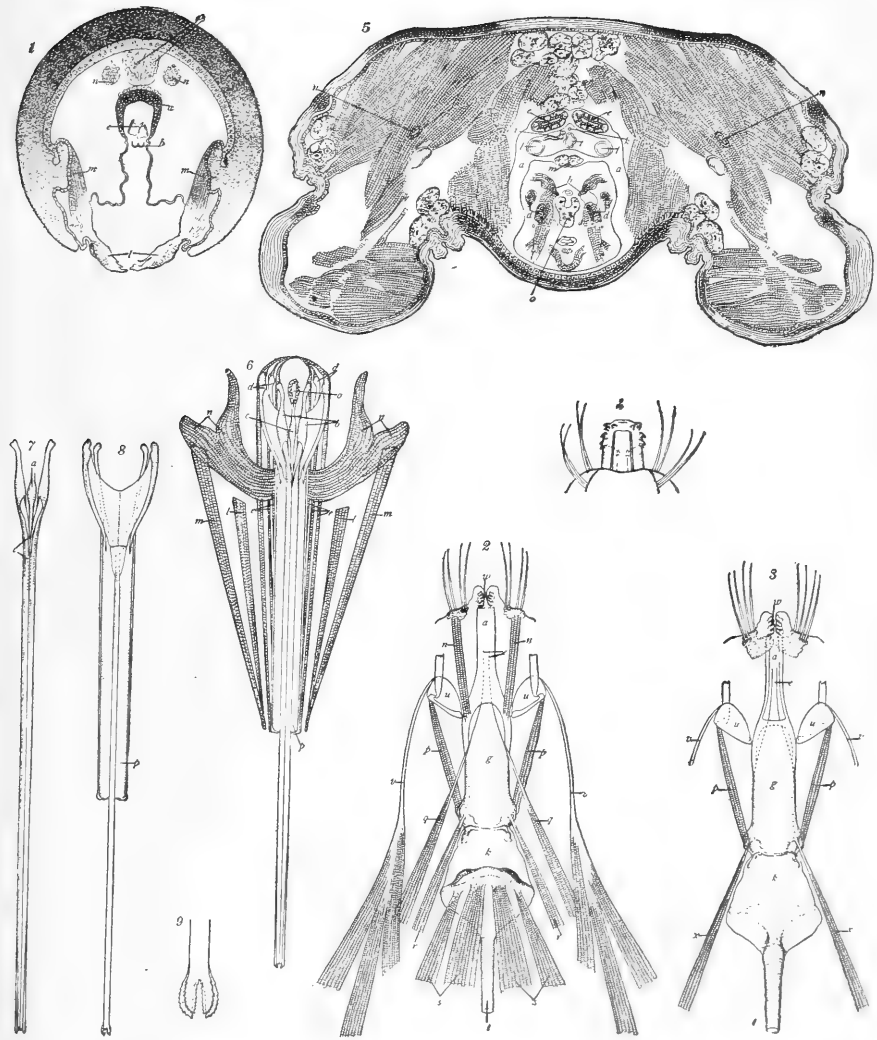

Plate LXI

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Transverse section through stomodaeum at anterior level of attachment of basal part of "mandibles" of Enderlein to lateral wall of head (a, buccal plate; b, dorsal element of piercers; c, salivary duct; d, ventral element of piercers); 2, transverse section through stomodaeum at anterior level of "mandibles" (e, pumping pharyngeal tube; other lettering as in 1); 3, transverse section through stomodaeum at posterior level of "mandibles" (lettering as in 1 and 2); 4, transverse section through stomodaeum in posterior region of buccal plate (aa, posterior arms of buccal plate; f, ridge on dorsum of pumping pharynx; other lettering as in 1 and 2); 5, transverse section through stomodaeum in region of anterior dorsal chitinous plate (g, pumping pharynx; h, piercer sheath; other lettering as in 1); 6, transverse section through stomodaeum immediately behind anterior chitinous plate (ii, tendons of dorsal retractors of buccal plate; other lettering as in 5); 7, transverse section through stomodaeum just after its separation from piercer sheath (lettering as in 6); 8, transverse section through anterior region of pharynx (k, pharynx); 9, transverse section through posterior region of pharynx behind first dorsal chitinous plate (jj, hollow tendons of central elevator muscles; k, pharynx)

(All drawings on this plate made with oil immersion and drawn to scale)

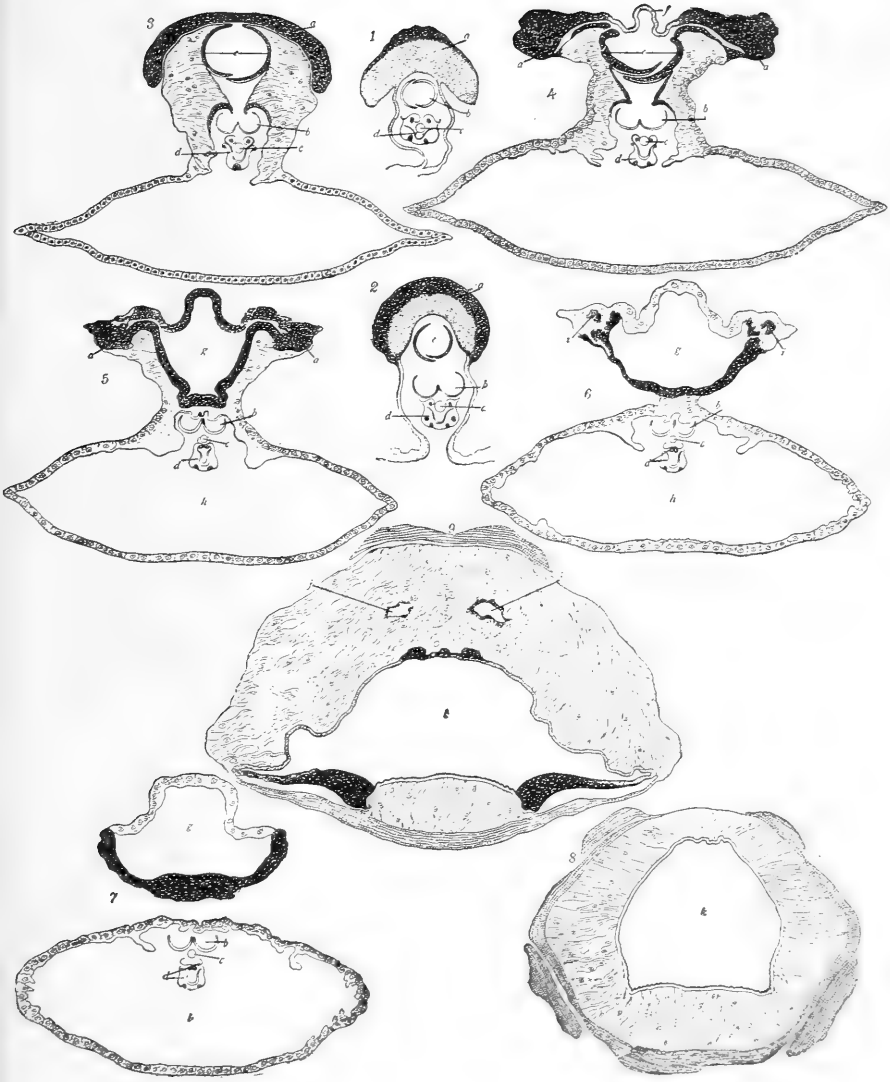

Plate LXII

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Transverse section through head, showing Pawlowsky's glands opening into piercer sheath (a, glands; b, piercer sheath); 2, longitudinal section through Pawlowsky's gland (drawn with oil immersion); 3, salivary glands in natural position (a, central aspect; b, lateral aspect); 4, horseshoe-shaped gland; 5, oblong-ovate gland; 6, anterior region of horseshoe-shaped gland and duct (drawn from gross specimen with oil immersion); 7, stomach (a, esophagus; b, mid-intestine; c, small intestine; d, region of plates; e, rectum; f, malpighian tubes); 8, transverse section through region of plates; 9, transverse section through rectum; 10, longitudinal section through abdominal segment (a, fat cells; b, oenocytes)

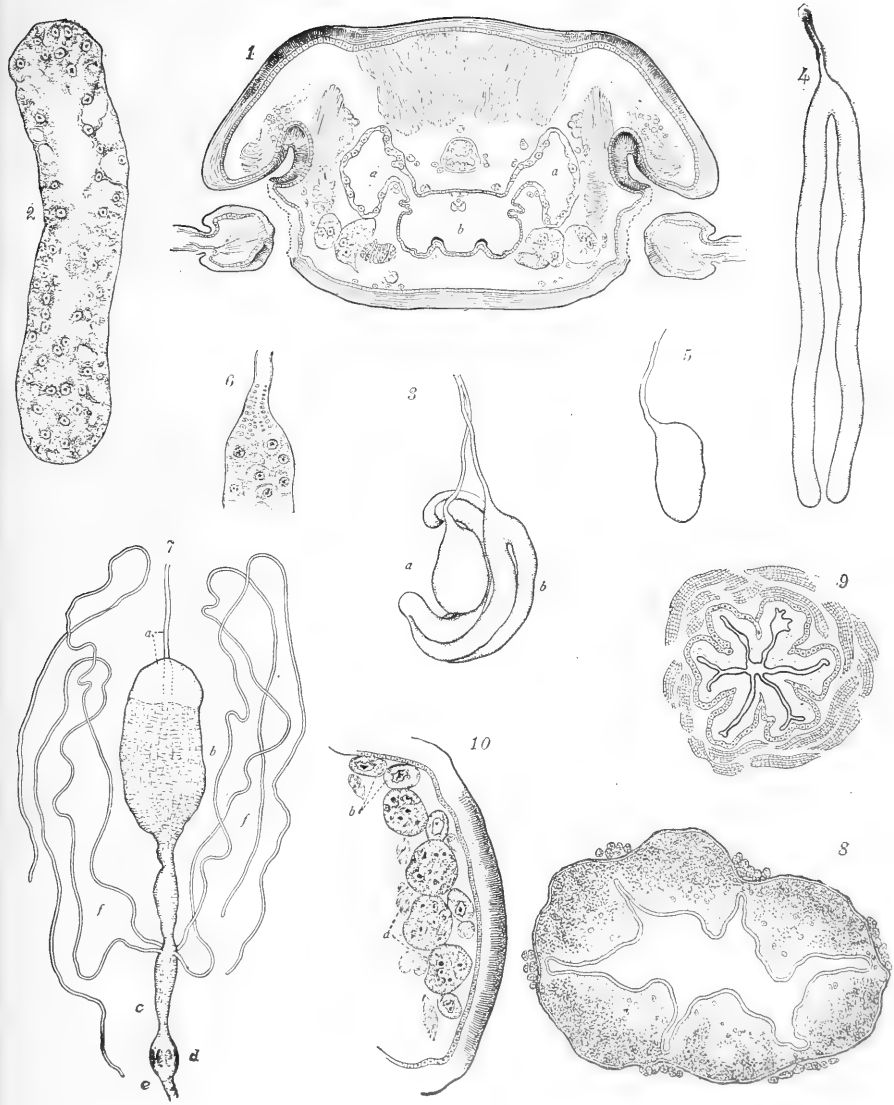
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PLATE LXIII

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Transverse section through stomach nine hours after feeding, x 192½ (a, region of section enlarged in 2); 2, region *a* of 1, x 600; 3, transverse section through intestine and reproductive organs of male, x 290 (a, intestine; b, seminal vesicles containing spermatophore; c, muscular part of ejaculatory duct; d, slender part of ejaculatory duct; e, vasa deferens; f, upper region of seminal vesicles which acts as reservoir for spermatozoa; g, malpighian tubes; h, trachea)

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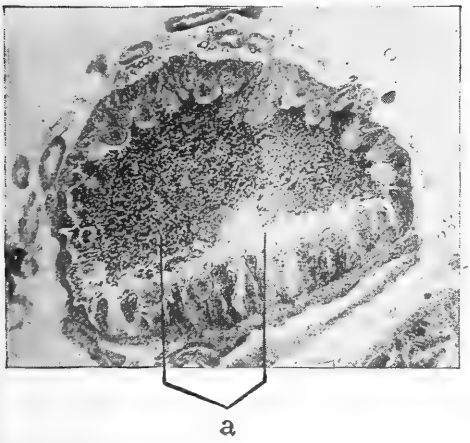

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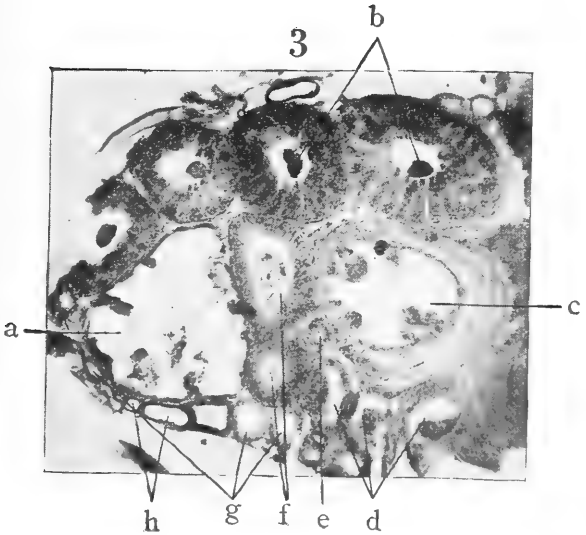

Plate LXIV

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Reproductive organs of male (a, testes; b, vasa deferentia; c, seminal vesicles; d, ejaculatory duct; e, penis; f, vesica penis; g, basal plate; h, parameres); 2, ectodermal reproductive organs of male in resting position, dorsal aspect (lettering as in 1); 3, ectodermal reproductive organs of male, vesica extended, ventral aspect (lettering as in 1); 4, posterior region of abdomen with vesica and penis ejected, lateral aspect (B, caudal aspect; l, upgrowth of ventral lamella of basal plate, corresponding to collar described by Nuttall in Pediculus; lettering otherwise as in 1); 5, transverse section through posterior end of abdomen of male (e, penis; f, vesica penis; ga, dorsal lamella of basal plate showing thickening of parameres; gb, ventral lamella of basal plate; i, muscles of parameres; j, retractor muscles of vesica; k, protractor muscles of basal plate); 6, transverse section of " spermatophore " (drawn with oil immersion)

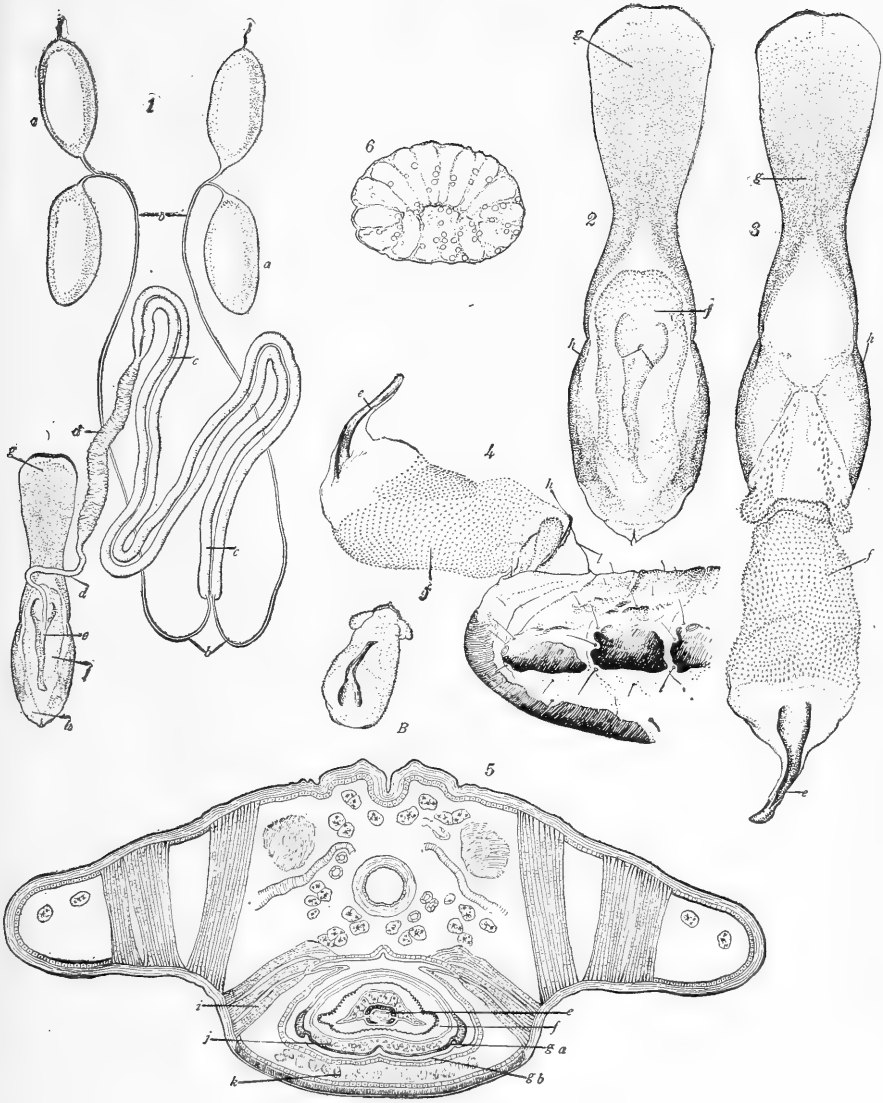
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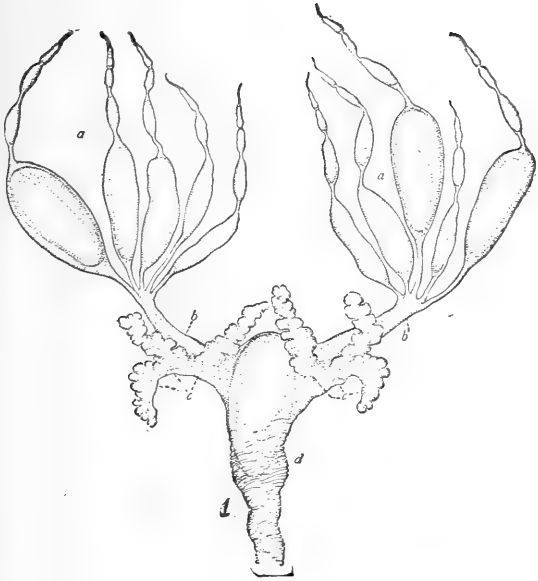
Plate LXV

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Reproductive organs of female (a, ovaries; b, oviducts; c, colleterial glands; d, uterus); 2, transverse section of part of wall of colleterial gland (drawn with oil immersion; a, trachea); 3, transverse section through anterior end of uterus; 4, transverse section through uterus posterior to the entrance of oviducts (a, secretion from colleterial glands); 5, transverse section through uterus in region of coil; 6, teeth of intima in 5 (drawn with oil immersion)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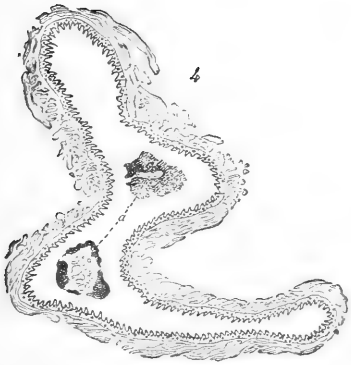
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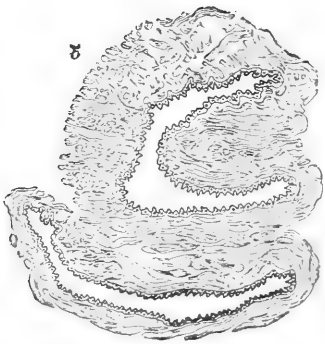
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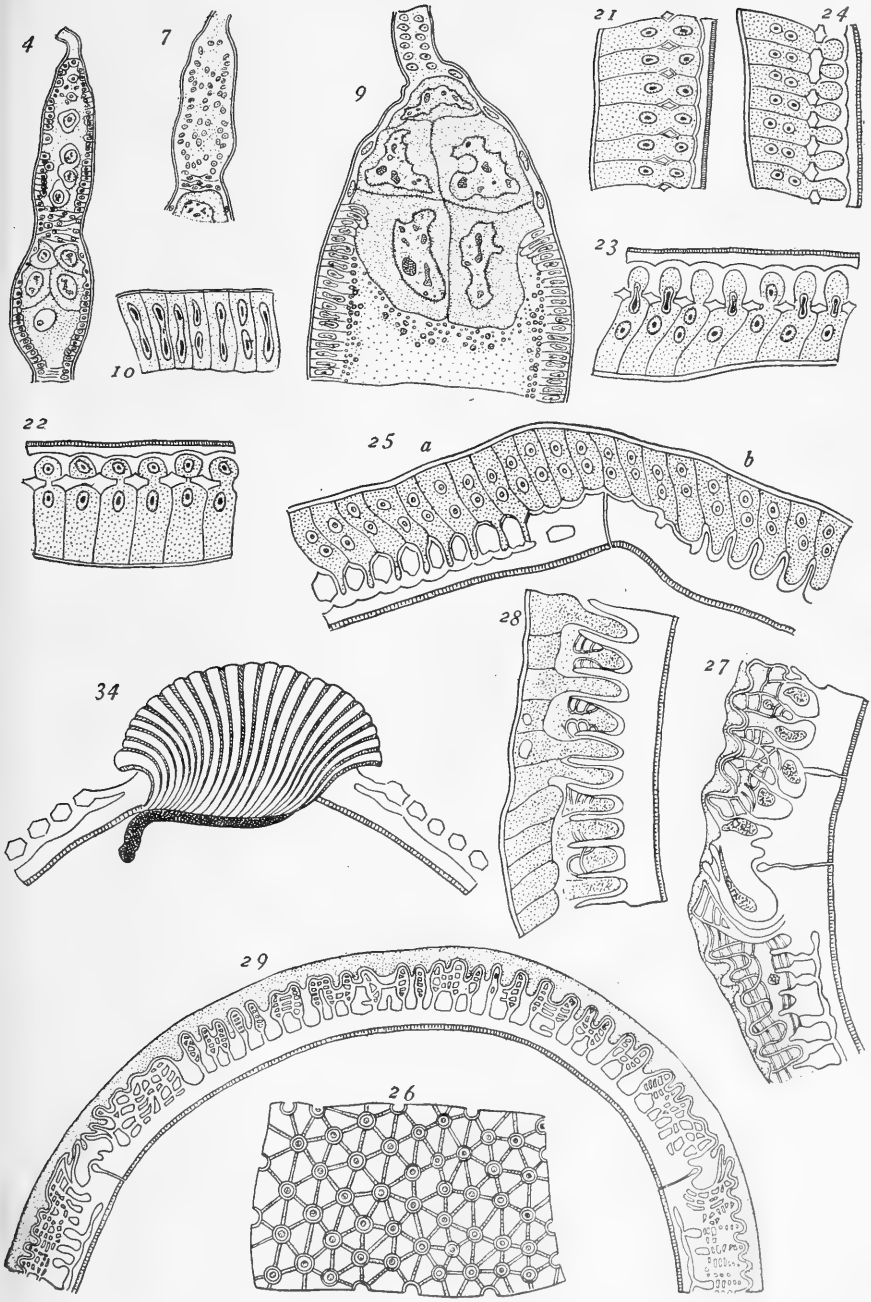
Plate LXVI

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

4, Longitudinal section through terminal chamber; 7, longitudinal section through terminal chamber; 9, longitudinal section through egg chamber; 10, cross section through follicle cells; 21–25, cross sections through follicle cells in different stages in formation of epichorion; 26, surface view of epichorion; 27 and 28, cross section through follicle cells in different stages in formation of epichorion; 29, section through egg cap; 34, longitudinal section through egg stigma

(Figures on this plate copied from Gross and numbered according to his arrangement)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CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

STUDIES IN POLLEN, WITH SPECIAL REFERENCE TO LONGEVITY

H. E. KNOWLTON

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

CONTENTS

STUDIES IN POLLEN,
WITH SPECIAL REFERENCE TO LONGEVITY

STUDIES IN POLLEN, WITH SPECIAL REFERENCE TO LONGEVITY

H. E. Knowlton

Altho much work has been done on problems concerned with pollination and fertilization, very little has been revealed as to the biology of the pollen itself. It is well known that the duration of viability of pollen varies with the species. It is found that corn and barley pollen only a few days old are unable to bring about fertilization, while date pollen may still effect fertilization after several years storage. The work done hitherto on this problem has consisted, for the most part, of mere observations, with no study of the underlying causes of pollen longevity. Aside from its scientific interest, the practical aspect of the question is important. The viability of pollen and practical methods of prolonging its life are of great importance to the plant breeder. With a knowledge of the most favorable conditions for pollen storage, it would be possible to cross plants blooming at different periods or those blooming in different parts of the world. This would permit more extensive crossing and a wider scope for the work of plant improvement.

The present work is a study of pollen and pollen longevity, with an attempt to determine, under different storage conditions, some of the reasons for pollen mortality. An endeavor was also made to discover practical methods of pollen storage.

EXTENT OF STUDIES

For a number of reasons, but particularly because it gave a fairly large quantity of pollen and a succession of blooms, snapdragon (*Antirrhinum majus* L.) was the chief material used in these experiments. The plants were grown in the greenhouse. For a short-lived pollen, corn (*Zea Mays* L.) was chosen. Some work was also done with apple (*Pyrus malus* L.).

Since the longevity of pollen was the primary interest, only those morphological and physiological studies were made which seemed to have a direct bearing on this problem. Extensive germination tests were made,

dealing with optimum temperatures and influence of stigma. Respiration, enzyme activity, moisture content, and carbohydrate reserves were also studied, both with fresh and with stored pollen. It was believed that these experiments would shed some light on the causes of death. Extensive storage experiments were made at different conditions of temperature and humidity. The influence of reduced pressures was noted and the influence of high and low temperatures on pollen viability was also studied.

Some pollen was also stored in carbon dioxide and some in oxygen.

HISTORICAL

Pollen germination

Much work has been done by previous investigators on pollen germination and on pollen-tube growth in artificial media. Generally, these workers have endeavored only to find the best medium for pollen germination. It is doubtful whether an artificial medium which in any way approximates conditions as found on the stigma and in the style has yet been found. The length of the pollen tubes developed on artificial media is generally insufficient for the complete penetration of the style. Without doubt, however, the physiology of germination is similar under both conditions. But in the later stages of growth within the style there is, according to East and Park (1918),[1] a more rapid elongation, while on artificial media the growth becomes progressively slower.

Van Tieghem (1869) seems to be recognized as the first investigator to have germinated pollen artificially, altho Von Mohl (1834) had previously germinated pollen of Morina in water. Von Mohl noted that in water the pollen tubes did not grow as long as they would need to grow under natural conditions.

Many species of pollen are not sensitive as to the kind or concentration of medium. Adams (1916) and Knight (1918) found that apple and other fruit pollen germinated over a wide range of concentrations of sugar, and even in water alone. A small amount of agar or gelatine added to the germinating medium improved germination with some species, according to Mangin (1886), Kny (1882), Garino-Canina (1914), and Andronescu (9115).

[1]Dates in parenthesis refer to *Bibliography*, p. 789.

Some species of pollen seem to require a definite kind of medium and a definite concentration. This is particularly true of the pollen of the Graminae. Andronescu (1915), after much experimentation, succeeded in germinating corn pollen in a 10-per-cent cane-sugar solution to which 0.7-per-cent agar had been added. Anthony and Harlan (1920) had great difficulty in germinating barley pollen. Other species seem to be equally sensitive.

Richer (1902) found that many species of pollen which normally do not germinate in a sugar solution do so when fragments of stigma are added. Other investigators (Molisch, 1893, and Lidforss, 1896) report that stigmas exert a strong stimulative action when added to the medium. Knight (1918) does not find this to be true with apple and Andronescu (1915) finds no influence with corn pollen. Molisch (1893) and Lidforss (1896) have noted chemotropic responses of the pollen tubes of some species to sugar, diastase preparations, and egg albumen.

Several enzymes are present in the pollen grain which function in making the food reserves available during germination and tube growth. Van Tieghem (1869) demonstrated the presence of invertase in pollen grains. Strasburger (1886) noted that pollen, growing in a starch paste, secreted amylase. Green (1894) found that amylase was widely distributed in pollen grains, and invertase less so. During germination, the quantity of both enzymes is considerably increased. Sometimes the resting grain contains no detectable amylase; but the enzyme makes its appearance on absorbing sugar from the medium.

Optimum temperatures for germination of pollen vary greatly, altho few workers have investigated this phase thoroly. Manaresi (1912) found that the best germinating temperature for the pollen of certain species of fruits was approximately 15° C. According to Popenoe (1917), the optimum temperature for mango pollen is about 25° C., with no germination below 16° C. Sutton and Wilcox (1912) found that the optimum temperature for the germination of tomato pollen was about 34° C., and for cucumber pollen about 27° C. Martin and Yocum (1918) state that the best temperature for apple-pollen germination is from 22° to 25° C. From these results we may conclude that the optimum temperature for pollen germination varies with the species. This is to be expected, as the plants themselves have different growth optima.

As a rule, light has no effect on germination, altho Sandsten (1910) found that with tomato pollen it was increased 25 to 50 per cent in sunshine. This increase, however, may be due to temperature effect.

Without doubt, the rôle of osmotic pressure in pollen germination has been overemphasized. Martin (1913) has attempted to determine the osmotic pressure of pollen grains. By means of the plasmolytic method, using different concentrations of cane sugar, he found the osmotic pressure of pollen of *Trifolium pratense* to be 165 atmospheres. His data show, however, that equivalent concentrations of different sugars produce widely different effects. He explains this on the basis of differences in the permeability of the sugars. Lloyd (1916, 1917) has presented data to show that, in the pollen of the sweet pea, it is the colloids of the grain that are more important. He concluded that " the living protoplasm as such behaves towards acids and alkalis in a manner sufficiently like that of gelatine to warrant the view that imbibition is a factor in growth." Osmotic factors are probably important in those species of pollen which do not germinate over a wide concentration of medium, as, for example, in the Graminae.

Duration of stigma receptivity

Horticulturists and investigators have generally assumed that a stigma is receptive from about the time the flower opens until the petals fall. As far as could be determined, there is no experimental evidence for this. Dorsey (1919) finds that in the native species of plum, the stigma, under normal conditions, remains receptive for about a week, but begins to turn brown after from three to five days. The styles begin to abscise about two weeks after blooming, but the abscission layer becomes very distinct in some varieties after eight days. Dorsey believes it doubtful whether the pollen tube is able to pass this abscission layer, for if pollination occurs late in the receptive period, only favorable growing conditions will allow the tube to pass the abscission layer before the style drops. As the petals fall from three to four days after blooming, it would seem that the duration of stigma receptivity is longer than that of the bloom. Undoubtedly, however, little pollination occurs after the petals have fallen, for bees seldom visit such flowers.

Anthony and Harlan (1920) worked on the period of receptivity of barley stigmas. In these investigations, flowers were pollinated each

day for six days. The percentage of fertilizations increased for two days, but from this time there was a gradual decrease until, on the sixth day, no pollinations brought about fertilization.

Pollen longevity

A considerable number of observations have been made by various workers on the life duration of pollen. However, as far as can be found, few carefully controlled experiments have yet been conducted.

The earliest reference to pollen longevity is in regard to date pollen. Kämpfer (1712) states that, if kept in a dark place, it is capable of fertilization the following year. Swingle (1904) writes that the Arabs make a practice of conserving, for use in the following year, a few bunches of staminate flowers, which are put in tight paper bags and kept in a dry, cool place. Bastin (1910) asserts that there is a tradition that date pollen will remain viable for fifteen years or even longer.

Gleditsch (1751) and Koelreuter (1797) state that the pollen of *Chamaerops humilis* will live for several weeks. The conditions under which the pollen should be stored are not stated, however.

Gärtner (1844) was successful in shipping the pollen of cycads, palms, and orchids. The longevity of many species varied from one to nine days. Gärtner found no relation between longevity of pollen and length of receptivity period of stigma.

According to Mangin (1886), the duration of life of the pollen of twenty different species of plants varied with the species; and among these the pollen of *Oxalis acetosella* lived for only one day, while that of *Picea excelsa* lived for eighty days, and that of *Antirrhimum majus* for forty-three days. The conditions of storage were not stated.

Sandsten (1910) found that the vitality of pollen was little affected by temperatures ranging from 25° to 55° C. in a dry atmosphere. A saturated atmosphere was injurious. Apple pollen was still alive after six months storage in a dry place at a temperature of from 8° to 26° C.

Molisch (1893) stored different species of pollen in watch glasses at room temperature and humidity. Longevity of pollen varied from two to six weeks, depending on the species.

Pfundt (1910) has done extensive work on the effect of moisture on pollen longevity. Pollen from one hundred and forty species of plants was subjected to different percentages of moisture at a temperature

ranging from 17° to 21° C., in darkness. Altho there were some exceptions, the duration of life was longest at 30 per cent humidity or in a perfectly dry atmosphere. Some of his data are given in table 1:

TABLE 1. SOME OF THE RESULTS OF PFUNDT'S INVESTIGATIONS OF THE EFFECT OF MOISTURE ON POLLEN LONGEVITY

Species	Per cent of moisture			Over H_2SO_4
	90	60	30	
Aesculus hippocastanum	6 days	17 days	72 days	72 days
Alisma plantago	1	1	1	1
Alnus glutinosa	32	46	59	53
Ampelopsis quinquefolia	6	11	23	19
Aquilegia vulgaris	5	14	84	92
Clematis integrifolia	6	24	89	103
Cornus mas	31	59	74	59
Corylus Avellana	.....	.....	.....	65
Digitalis purpurea	9	13	43	172
Hippuris vulgaris	5	5	3–5	2
Impatiens Sultani	13	3	29	23
Lilium bulbiferum	8	31	142	142
Melilotus albus	6	14	96	73
Mercurialis perennis	8–10	29	58	72
Oenothera biennis	2	6	8	6
Pandamus furcatus	11	30	92	92
Papaver hybridum	33	17	49	49
Pinus montana	.....	.....	.....	272
Pinus sylvestris	.....	.....	.....	279
Pyrus malus	.....	.....	.....	70
Plantago media	3	12	50	68
Poa compressa	1	1	1	1
Potentilla argentea	2	5	21	44
Prunus cerasus acida	.....	.....	.....	81
Prunus padus	14	22	181	181
Salix alba	.....	.....	.....	57
Salix gracilis	12	18	38	52
Secale cereale	12 hours	12 hours	12 hours	12 hours
Solanum dulcamara	7 days	9 days	41 days	41 days
Tradescantia Virginica	2	3	31	40
Tulipa Gesneriana	23	43	108	92
Ulmus campestris	6	9	22	17
Viburnum opulis	.....	.....	.....	164
Vicia faba	.....	.....	.....	21
Viola odorata	19	28	217	235

Crandall (1913), storing pollen in covered petri dishes, found that apple pollen one month old would not germinate, but that when eleven days old it was still capable of fertilization. Strawberry pollen three

hundred and seventy-seven hours old, fertilized successfully, and sweet-pea pollen fertilized after twenty-three days.

Kellerman (1915) shipped Citrus pollen from Florida to Japan, using four methods of storage: (1) in cork-stoppered vials, (2) in cotton-stoppered vials, (3) anthers in glass tubes exhausted to 10 millimeters pressure, and (4) anthers in dried glass tubes exhausted to 0.5 millimeter pressure. During shipment, which covered a period of from four to six weeks, the pollen was kept at a temperature as near 10° C. as possible. Both the third and fourth methods were successful, but the fourth was the more so.

Andronescu (1915) worked on the longevity of corn pollen. Corn pollen kept in a dry oven, at 42° C., was killed in twenty minutes, while in a saturated atmosphere, under the same conditions, there was 32 per cent of germination. Pollen exposed in the laboratory died in two hours; uncovered, out of doors, it lived for four hours; in 60-per-cent moisture, for six hours; in 90-per-cent moisture, for forty-eight hours. Pollen in sealed tubes lived for twenty-four hours.

McCluer (1892), also working with corn pollen, found that if kept dry it retained its vitality for several days.

Roemer (1915) stored pollen both in cotton-stoppered test tubes and in gelatine capsules. He concluded that pollen remained viable longest under low temperature (5°–10° C.) and low moisture conditions.

Tokugawa (1914), using species of Lycoris, Torenia, and Narcissus, and Simon (1911), using pumpkin, also found that the pollen lived longest in a dry atmosphere. The pumpkin pollen lived for five weeks in a sealed vessel containing anhydrous calcium chloride. Adams (1916) found that, in a dry condition, apple pollen kept for three months; pear pollen, for ten weeks. Strawberry, loganberry, and raspberry pollen were dead after two months and black-currant pollen was dead after eleven weeks.

Horsford (1918) preserved pollen of *Lilium auratum* until the following spring by wrapping it in several sheets of paraffin paper and storing it in a warm, dry place. It rapidly lost its vitality on exposure to air.

Anthony and Harlan (1920) worked with barley pollen. They used both artificial methods of germination, and germination directly on the stigma, as tests of viability. Pollen twenty-four hours old produced a greatly decreased percentage of fertilization, while pollen forty-eight hours old was incapable of effecting fertilization. Pollen stored under conditions which retarded evaporation remained viable for the longest time.

It is evident, from a study of these experiments, that the pollen of most species remains viable longest under conditions of low temperature. Altho there are few available data, the indications are that the optimum moisture conditions vary with the species.

In all of the experiments mentioned in the foregoing paragraphs, artificial germination, except as otherwise noted, was the only test of viability used in the investigations. As will be shown by the author's experiments, this is not always a proof of ability to bring about fertilization.

Possible causes of death of pollen

As far as the writer has learned, Andronescu (1915) is the only investigator who has advanced a theory to explain the cause of death of pollen. He found that corn pollen stored out of doors lost 48 per cent of its moisture in two hours and 52 per cent in twenty-four hours. Since he found also that pollen lived longer at higher humidities, he concluded that death is the result of desiccation. Pfundt (1910), however, determined that the range of moisture required is wide, depending on the species: some live longer at low, others at high humidities. It is not possible to conclude, therefore, that desiccation is always the cause of death.

Investigators generally agree that the duration of life is longer at fairly low temperatures. This is to be expected, as physiological activities are slower.

Altho pollen and seeds differ morphologically as well as in function, it was thought that the cause of death in each might be similar. A brief discussion of the causes of death in seeds is, therefore, desirable.

Acton (1893) found that thirty-years-old wheat which had lost its germinative power, contained about the same amount of stored food but less water than did new grains, and that its amylase and proteolytic enzymes had also been destroyed. On the contrary, Brocq-Rousseu and Gain (1909) state that amylase and oxidase were present in wheat grains ranging from twenty-five to eighty years old. White (1909) states that amylase was present in fairly large quantities in old seed of wheat, barley, oats, rye, and corn. The age of the seeds tested ranged from two to twenty-one years. The addition of amylase did not cause dead seeds to germinate.

Crocker and Harrington (1918) and their coworkers found that, in some seeds, catalase activity is correlated with physiological activity and

decreases with age. Crocker and Groves (1915) advance a theory that the loss of viability of seeds in storage is due to a slow coagulation of the proteins in the plasma of the embryo. They applied Buglia's (1909) time-temperature formula for protein coagulation and found it applicable for a temperature-life-duration formula for seeds. This formula is

$$T = (a-b) \log Z$$

in which T represents the temperature and Z the time of heating, and a and b are constants. Several factors, such as the increase in acidity of the seed, the redispersal of proteins in seeds of high water content, and variability in the water content, may limit the general application of this formula. A slight error in a and b gives a relatively large error for a life duration at low temperatures.

There are no records of attempts to determine whether the death of pollen is due to any of these causes, that is, exhaustion of stored food, destruction of enzymes, or coagulation of proteins.

EXPERIMENTAL WORK

Description of pollen

Pollen of snapdragon (Antirrhinum majus L.)

The pollen of snapdragon is produced very abundantly. It is yellow in color and is covered with a gummy substance which causes the grains to adhere to one another. As this sticky pollen cannot be wind-carried, cross-pollination is effected by bees and other insects. The pollen is rather below the average in size; is oval in shape, when dry, but when turgid, in a sugar solution, is nearly spherical. Dry pollen measures 26.5μ in length, and 15.3μ in width; when turgid, the average diameter is 24μ. Halsted (1889) has noted a similar change in shape with other species of pollen. When dry, the position of the germ pores is marked by three long folds in the wall. These folds are less distinct when the cell becomes turgid.

Analyses of fresh pollen show that cane sugar is the reserve carbohydrate, the amount present, expressed in percentage of fresh substance, varying from 8 to 10 per cent. Small amounts of reducing sugars are also present, but no starch was detected.

Other investigators have made chemical analyses of pollen. Van Tieghem (1869) observed that some species of pollen store cane sugar.

Von Planta (1885) found 14 per cent of cane sugar in Corylus pollen and 11 per cent in Pinus pollen. Mangin (1886) noted that Betula and certain Coniferae pollens have reserve starch, while others (Narcissus) have stored sugar only. Green (1894) stated that many species of pollen contain starch, glucose, maltose, and cane sugar. In the immature pollen grains of wheat, Eckerson (1917) at first found glucose, and later, starch appeared. Martin and Yocum (1918) state that, at pollination time, apple pollen contains proteins and small amounts of sugar. According to Green (1894) and others, these organic reserves are broken down by appropriate enzymes during the germination of the pollen.

Determinations show a surprisingly small water content, only 10 to 20 per cent being present. The amount varies under different conditions and in different seasons.

Pollen of corn (Zea Mays L.)

Corn pollen is produced in large quantities. This fact was one of the reasons for its selection as a material for testing in these experiments. Under favorable conditions, in the early morning, it was very easy to collect from 25 to 30 grams of pollen in a cornfield. This allowed analyses to be made, which could not have been done with the more scanty pollen of other species. Corn pollen seems very dry, does not adhere, and is consequently wind-borne.

Fresh corn pollen is oval to round in shape, altho elongated grains are often noticed. On exposure, they become shrunken. Corn pollen is larger than Antirrhinum, measuring 106μ by 120μ. When the microscope is properly focused, circular germ pores, one to three in number, can be seen. These pores resemble bordered pits of wood tissue.

Unlike Antirrhinum pollen, starch is the storage carbohydrate of corn pollen, whole pollen grains often staining a deep blue in iodine solution. Other grains did not stain so deeply, indicating that they contained less starch. Chemical analyses showed about 10 to 15 per cent starch, expressed in percentage of fresh substance. The table given by Andronescu (1915) shows 39 per cent of total carbohydrates. No starch analyses were made by him.

Altho corn pollen is wind-borne and seemingly dry, the moisture content is very high. Determinations made by the writer showed that it ranged from 50 to 65 per cent, depending on the amount of moisture in the air,

the maturity of the tassel, and the amount of water available to the plant. In illustration of this, pollen freshly gathered in the field showed 52 per cent of water, while pollen gathered in the laboratory, from tassels standing in a jar of water, contained 63 per cent of moisture. Andronescu (1915) states that corn pollen has an average moisture content of about 57 per cent. As will be shown later, it loses moisture rapidly on exposure to conditions of low humidity.

Method of pollen germination

In all artificial germinations the following method was used: A small quantity of pollen was placed in a drop of sugar solution or sugar-agar solution, on a cover glass. The cover glass was then inverted over a Van Tieghem cell which contained several drops of the same solution. Vaseline was placed around the edges of the cell to secure the cover glass and to prevent evaporation

Germination of Antirrhinum pollen

Antirrhinum pollen germinated well in a cane-sugar solution, very high percentages of germination resulting. There was no very great sensitiveness as to concentration. At one time the highest percentage of germination would result at one concentration, at other times, at another. In general, the best germination was obtained in a 15- to 25-per-cent cane-sugar solution. There was a small percentage of germination in water. The range of concentration at which germination occurred is shown in table 2. In other experiments a higher percentage of germination, even as high as 80 to 90 per cent, was obtained.

TABLE 2. GERMINATION OF ANTIRRHINUM POLLEN

Cane sugar (per cent)	5	10	15	20	25	30
Germination (per cent)	38	18	42	70	32	3

As the germ-tube growth progressed, a thickening of the tube wall occurred at several points back of the growing tip. These areas increased in thickness until finally the whole tube was plugged with callose. These callose plugs can be seen in unstained slides, but a short immersion in

a weak aniline-blue solution brings them out more clearly. In pollen tubes of apple, the plugs are more numerous than in Antirrhinum.

The germination of Antirrhinum pollen was greatly stimulated by the addition of a minute amount of the crushed stigma of Antirrhinum. Pollen in a sugar solution showed germ tubes appearing after one and one-half hours. The addition of a piece of the stigma to the same concentration of sugar so stimulated germination that within one hour the germ tubes were from one to four times the diameter of the grains in length. Marked chemotropism also resulted, the germ tubes growing toward, and even penetrating, the stigma tissue. No effect was obtained by the addition of either geranium or petunia stigmas, however.

Even pollen from anthers that had not dehisced was germinated. Pollen from anthers which would have dehisced three days later showed no germination after two hours, in contrast to mature pollen, which showed a 60-per-cent germination. After twenty hours, the immature pollen showed a 65-per-cent germination, while the mature pollen gave an 85-per-cent germination. The germ tubes of the mature pollen were longer. A small percentage of germination was obtained with more immature pollen, but it was very slow and weak. Very immature grains, below normal in size, seemed to grow larger when placed in a nutrient solution, but no germination took place. It is apparent, then, that pollen matures several days before the anthers dehisce.

Optimum temperatures for Antirrhinum-pollen germination were determined. The pollen was taken from the same anther. The results, given in table 3, are the averages of six cultures for each temperature, the media being cane-sugar solutions:

TABLE 3. ANTIRRHINUM POLLEN GERMINATION AT DIFFERENT TEMPERATURES

Temperature (centigrade)	21°	26°	29°	33°
Germination (per cent)	36	56	22	15

Under the conditions of the experiment, it may be concluded that the optimum temperature for the germination of Antirrhinum pollen is about 25° C.

Germination of corn pollen

Great difficulty was experienced in the first attempts to germinate corn pollen. There was no germination in water, altho Jost (1905) claims to have succeeded in obtaining it. Various kinds and concentrations of sugar were tried unsuccessfully. Pieces of stigma and decoctions of stigmas had no effect. Occasionally, several grains developed short germ tubes, but there was no general germination.

Later experiments were more successful. A 20-per-cent germination was obtained in 10-per-cent cane sugar plus 0.7-per-cent agar, as recommended by Andronescu (1915). By varying the concentration, even better germination resulted, as is shown in table 4:

TABLE 4. GERMINATION OF CORN POLLEN

Medium		Germination
Agar +	Cane sugar	
Per cent	*Per cent*	*Per cent*
1.0	15.0	56
0.7	15.0	62
0.7	20.0	18
0.5	17.5	30
0.5	15.0	3

Germination is so rapid that after two or three minutes the protrusion of the tubes may be observed. The subsequent elongation was slower. Protoplasmic streaming was plainly visible in the germ tubes. After twenty-four hours, the germ tubes ranged in length from one to seven times the diameter of the grains.

Good germination was not obtained consistently. At times, the results from a certain concentration of solution were excellent; again, the same strength of solution failed to induce germination. Apparently the water relations were very delicate and the concentration had to be exactly correct before germination could take place. This is a common difficulty with the pollen of Graminae, according to other investigators (Anthony and Harlan, 1920). Martin (1913) found this to be true also of the pollen of *Trifolium pratense.*

As the water content of corn pollen is high, it is probable that osmotic pressure plays an important part, both in the swelling of the grain and in its subsequent growth. This idea is strengthened by the fact that a definite concentration of sugar is necessary, any departure from which results in failure to germinate or in abnormal germination. It is difficult to understand why a definite concentration would be necessary if colloidal imbibition played the main rôle. On the other hand, the water content of Antirrhinum pollen is low and the pollen germinates in almost any concentration of sugar. Imbibition is probably more important here than is osmosis.

Results were so variable that it was thought best not to use artificial germination as a test of viability in the experiments on longevity of corn pollen. Only fertilization tests were employed, therefore.

Apple (*Pyrus malus* L.) pollen resembles Antirrhinum pollen in that it is easy to germinate and is not sensitive as to the concentration of sugar solution, as is indicated in table 5:

TABLE 5. GERMINATION OF APPLE POLLEN (25° C.)

Sugar solution	Germination	Length of pollen tubes *
Per cent	*Per cent*	
2.5	1	Short
5.0	2	Short-long
7.0	8	Short-medium
10.0	12	Short-medium
12.0	15	Short-long
15.0	30	Short-long
17.0	40	Short-long
20.0	20	Short-medium
22.0	7	Short
25.0	30	Short-medium
28.0	30	Short-medium
30.0	25	Short-long

*Short signifies a length of from 1 to 5 pollen-grain diameters; medium, a length of from 5 to 10 pollen grain diameters; and long, a length of from 10 to 25 pollen-grain diameters.

Altho Knight (1918) found that the addition of pieces of the stigma to the medium exerted no favorable action, the author thus procured stimulation repeatedly, and even chemotropism. It was not as pronounced as with Antirrhinum pollen, however.

Duration of receptivity of the stigmas of Antirrhinum

In any pollination experiment, data concerning the duration of stigma receptivity are important. Few investigators of pollination problems study this phase of the work, however. As has been mentioned, Dorsey (1919) determined this period for the plum, and Anthony and Harlan (1920) for barley.

In order to find out the length of time stigmas of Antirrhinum remain receptive, the following experiment was conducted. A large number of flowers were emasculated prior to the time the petals unfolded, and pollinations with fresh pollen were made at intervals up to several weeks after the opening period of the flowers. Results of this experiment are given in table 6:

TABLE 6. DURATION OF RECEPTIVITY OF ANTIRRHINUM STIGMAS

Day after flowers opened	Number pollinated	Number fertilized	Number not fertilized
Same day	11	9	2
5th	6	6	0
6th	6	6	0
8th	8	8	0
10th	11	10	1
14th	7	1	6
16th	5	3	2
18th	4	0	4
21st	11	2	9
23d	5	0	5
25th	5	0	5

Two weeks after pollination, capsules were produced, but these were smaller and contained a smaller number of seeds. The pistils of emasculated flowers, if the pollen was withheld for any length of time, grew to an abnormal size. After from fifteen to eighteen days, the pistils began to wither.

These results show that after ten days the percentage of fertilization decreased, altho several fertilizations took place on flowers three weeks old.

The duration of receptivity of corn stigmas was not determined. It is generally understood by plant breeders, however, that corn can be pollinated successfully until the silks begin to wither.

Storage experiments with Antirrhinum pollen

Influence of temperature

The investigation of pollen storage, in 1915, consisted only of a study of the effect of different temperatures on pollen longevity. Both the germinative power on artificial media and the ability to actually fertilize

TABLE 7. ANTIRRHINUM POLLEN STORED AT 40° C. 1915

Age	Flowers pollinated	Seed capsules developed	Greatest germination	Sugar concentration in which maximum germination resulted	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	*Per cent*	
0	.....	.....	60	15	.....
3	1	1	80	20	.....
5	2	0	42	30	Short
10	5	1	54	25	Short
14	5	0	47	30	Short
21	3	0	65	20	Short–medium
28	7	1	60	25	Short–medium
42	3	0	30	20	Short

TABLE 8. ANTIRRHINUM POLLEN STORED AT 30° C. 1915

Age	Flowers pollinated	Seed capsules developed	Greatest germination	Sugar concentration in which maximum germination resulted	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	*Per cent*	
3	3	3	.....	.....	.....
5	6	2	35	25	Short–medium
10	3	0	2	25	Short
14	6	4	0	.....	.....
21	5	0	0	.....	.....
28	3	0	0	.....	.....

TABLE 9. ANTIRRHINUM POLLEN STORED AT 21° C. 1915

Age	Flowers pollinated	Seed capsules developed	Greatest germination	Sugar concentration in which maximum germination resulted	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	*Per cent*	
3	4	3	32	10	Short-long
5	7	4	.....	.....	.....
10	1	1	13	15	Short-medium
14	6	1	8	20	Short-medium
21	3	2	9	15	Short
28	4	1	27	25	Short
42	4	0	.....	.....	.....

TABLE 10. ANTIRRHINUM POLLEN STORED AT 0° C. 1915

Age	Flowers pollinated	Seed capsules developed	Greatest germination	Sugar concentration in which maximum germination resulted	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	*Per cent*	
3	7	5	9	15	Short-medium
5	7	4	40	25	Medium-long
10	4	4	72	20	Medium-long
14	3	2	.....	.....	.....
21	9	2	56	20	Short-long
42	6	2	12	25	Short
88	.....	.....	0	.....	.....

were used as tests of viability. Since concentrations in which maximum germination took place varied on successive days and with different samples of pollen, six concentrations of cane sugar were used for each test. Slides were examined after twenty-four hours. Pollen was stored in small stoppered bottles, one for each withdrawal.

TABLE 11. ANTIRRHINUM POLLEN STORED AT −18° TO −30° C. 1915

Age	Flowers pollinated	Seed capsules developed	Greatest germination	Sugar concentration in which maximum germination resulted	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	*Per cent*	
3	3	2	20	30	Short
5	8	2	47	20	Short–long
10	10	9	50	10	Short–long
14	6	4	35	25	Long
21	6	0	12	25	Short–medium
28	3	0	36	15	Short–long
42	3	1	20	20	Short–medium
88	.....	.....	26	30	.....

TABLE 12. ANTIRRHINUM POLLEN STORED AT −18° TO −30° C. 1917

Age	Flowers pollinated	Flowers fertilized	Germination	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	
7	6	6	30	Long
28	8	5	50	Short–long
42	10	10	60	Medium–long
77	5	5	60	Medium–long
105	6	4	50	Short–long
133	5	4	50	Short–long
161	5	3	50	Short–long
189	.....	.....	15	Short–medium
217	.....	.....	1	Short

In the 1917 experiment, pollen was still capable of fertilizing after storage for 161 days at −18° C. to −30° C. No other temperature experiments were performed that year.

These results show an increasing longevity as the temperature at which pollen was stored decreased. At 40° C., only three fertilizations resulted and artificial germinations showed a weak pollen-tube growth. At 30° C. there were more fertilizations, but germination was poorer. Storage conditions were more favorable at 21° C. At this temperature, the pollen

was still capable of fertilization after one month. Germination grew progressively weaker with increasing age. At 0° C., pollen remained viable for six weeks. Germination was better and pollen tubes grew longer than when stored at other temperatures. The pollen had not lost its germinative power after three months at −17° C. to −30° C. It may be concluded, therefore, that the lower the storage temperature, the longer Antirrhinum pollen remains viable.

These experiments also show that the optimum sugar concentration for artificial germination varies from 10 to 30 per cent.

Influence of carbon dioxide

Since Kidd (1917) had found that high percentages of carbon dioxide in the atmosphere depressed the respiration of the seeds and therefore increased the period of longevity, some pollen-storage experiments were made under these conditions in 1917. Sealed glass tubes containing 15 per cent of carbon dioxide were used as receptacles.

The results, tho inconclusive, seemed to show that Antirrhinum pollen will remain viable longer in an atmosphere containing 15 per cent of carbon dioxide than in normal air. Similar conditions will result, however, whenever pollen is stored in containers merely sealed, for, due to respiration, the carbon dioxide content of the inclosed atmosphere will increase.

In 1917, some pollen was stored in pure carbon dioxide. Sealed glass tubes were again used as containers. The results are given in table 13:

TABLE 13. ANTIRRHINUM POLLEN STORED IN PURE CARBON DIOXIDE AT 10°–20° C. 1917

Age	Pollinated		Fertilized		Germination		Average length of pollen tubes	
	In air	In carbon dioxide	In air	In carbon dioxide	In air	In carbon dioxide	In air	In carbon dioxide
Days	*Number*	*Number*	*Number*	*Number*	*Per cent*	*Per cent*		
7	5	9	5	6	50	60	Short	Medium–long
21	12	15	10	9	20	60	Short–medium	Medium
28	.....	15	.....	11	60	40	Medium–long	Medium
42	4	7	3	6	60	60	Medium–long	Short–medium
49	.....	7	.....	4	.....	60	.....	Medium
63	.....	10	.....	9	.....	10	.....	Short–medium
86	.....	6	.....	4	.....	25	.....	Short–medium
105	8	4	4	4	40	50	Medium	Short–long
121	6	8	6	8	.....	.....	.....	.....

Pollen remained viable for four months in an atmosphere of carbon dioxide. In this atmosphere, the small amounts of respiration that occurred must have been anaerobic. Kidd (1917), however, has shown that carbon dioxide has a retarding effect on both aerobic and anaerobic respiration.

Influence of reduced pressure

Kellerman (1915) found that Citrus pollen remained viable longer under low atmospheric pressures. Some experiments were made in 1917 to determine whether this was true also with Antirrhinum pollen. The pollen was stored in sealed glass tubes, with the atmospheric pressure reduced to 100 millimeters.

TABLE 14. ANTIRRHINUM POLLEN STORAGE AT A PRESSURE OF 100 MILLIMETERS COMPARED TO STORAGE AT NORMAL ATMOSPHERIC PRESSURE, AT 0° C. 1917

Age	Flowers pollinated		Seed capsules developed		Greatest germination		Average length of pollen tubes	
	In normal pressure	In reduced pressure	In normal pressure	In reduced pressure	In normal pressure	In reduced pressure	In normal pressure	In reduced pressure
Days	*Number*	*Number*	*Number*	*Number*	*Per cent*	*Per cent*		
7	3	9	3	8	45	35	Short–long....	Medium–long
28	.....	9	.....	7	10	60	Medium–long.	Medium–long
42	13	3	12	3	50	40	Medium–long.	Medium–long
77	3	2	3	2	70	15	Medium–long.	Short–medium
105	5	6	2	5	60	0	Medium–long.	.....
133	4	.....	4	.....	60	0	Medium–long.	.....
161	3	.....	3	.....	50	.....	Short–medium.	.....

Under normal atmospheric pressure, pollen remained viable longer than under reduced atmospheric pressure. Another series, at 10° C., gave similar results. Dude (1903) also found this to be true with certain kinds of seeds. He attributed the lessening of longevity to the injurious products formed in anaerobic respiration.

Influence of storage in pure oxygen

Storage in oxygen was studied in 1917, with results as shown in table 15. The pollen was stored in sealed glass tubes.

Due to the absence of the author during the war, no tests were made from the 196th day to the 670th day. Altho there was weak germination after the long storage, it is significant that there were no fertilizations. Undoubtedly, respiration was more active; perhaps, also, there was an

exhaustion of stored food. Since more favorable results were obtained in normal air than in pure oxygen, it would appear that normal atmosphere is more favorable to the prolongation of viability.

TABLE 15. ANTIRRHINUM POLLEN STORAGE IN PURE OXYGEN COMPARED TO STORAGE IN AIR (10°–22° C.). 1917

Age	Flowers pollinated		Seed capsules developed		Percentage of germination		Average length of pollen tubes	
	In air	In oxygen	In air	In oxygen	In air	In oxygen	In air	In oxygen
Days	*Number*	*Number*	*Number*	*Number*	*Per cent*	*Per cent*		
7	9	3	8	3	20	65	Medium–long..	Long
14	.....	.....	.....	.....	50	.....	Long.....	.....
28	.....	6	.....	5	.....	40	.....	Medium–long
35	7	.....	6	.....	40	.....	Short–long....	.....
42	.....	6	.....	5	.....	60	.....	Medium–long
56	12	.....	11	.....	40	.....	Medium–long..	.....
98	.....	5	.....	3	.....	40	.....	Medium long
112	4	.....	1	.....	30	.....	Medium–long..	.....
126	.....	6	.....	2	.....	40	.....	Medium–long
140	2	.....	2	.....	30	.....	Short–long....	.....
152	.....	5	.....	2	.....	30	.....	Short–long
168	.....	.....	0	.....	5	.....	Short.....	.....
180	.....	.....	.....	.....	.....	10	.....	Short–medium
196	.....	.....	0	.....	0	.....	.....	.....
670	8	.....	0	.....	50*	10*	Short–medium.	Short.

*Piece of stigma added. No germination occurred in absence of stigma.

From the results of all these storage experiments, it may be concluded that Antirrhinum pollen remains viable longest at low temperatures. Moisture conditions, provided they are not too high, are not important. Storage under low atmospheric pressures does not yield good results. Pollen remains viable longer in normal atmosphere than in pure oxygen. There is some evidence that an atmosphere of pure carbon dioxide or one containing large percentages of it favors longevity. The results obtained in 1917 were better than in previous years, a fact which may be due, in part, to the sealed glass tubes used as storage containers, but which is more probably due to the greater virility of the pollen produced in 1917. The author wishes to emphasize the fact, mentioned by other investigators (Kellerman, 1915), that pollen varies greatly. Many data had to be discarded because of this uncontrollable factor.

The writer has demonstrated that Antirrhinum pollen can be stored a longer time than forty-three days, which was the limit reported by

Mangin (1886). If the temperature remains low, Antirrhinum pollen should remain viable for five months or longer, tho the variability of pollen may necessitate a qualification of this statement.

Possible causes of death of Antirrhinum pollen

Loss of moisture

As Antirrhinum pollen has a low water content, it was believed that moisture conditions would not affect longevity to any great extent. Under very humid conditions, however, moisture collected on the pollen and contaminations by molds soon resulted.

To determine whether the Antirrhinum pollen would lose moisture rapidly, a small quantity of pollen was spread on a watch glass, weighed, and placed in the incubator at 25° C., where the humidity ranged from 20 to 40 per cent. Weighings were made daily. At the end of seventy days the weight was practically the same as at the beginning. Slight fluctuations occurred during this period, as the humidity within the chamber varied. Since little moisture loss occurred, this sample of Antirrhinum pollen must have been in equilibrium with the atmosphere at this particular humidity. The fact that the pollen had lost little water, altho exposed for seventy days to an atmosphere low in humidity, would indicate that moisture loss does not condition the duration of viability.

Respiration experiment

Exhaustion of the stored carbohydrates suggested itself as a cause of death. Since the water content is low, metabolic processes, and particularly respiration, should be less active. To determine the truth of this, an attempt was made to study respiration. Several methods were tried, but none were successful because the amount of carbon dioxide given off was so very small. Difficulties were enhanced by the necessarily small amounts of material. The conclusion drawn from these attempts was that the respiration rate of Antirrhinum pollen is very low — probably comparable to that of seeds having a low moisture content.

Depletion of cane sugar

Altho respiration seemed a negligible factor, it was deemed advisable to make carbohydrate analyses of fresh and stored pollen, in order to

determine whether there was any diminution. Sachsse's method was used. Pollen was stored at room temperature in sealed bottles. The results are given in table 16:

TABLE 16. CARBOHYDRATE ANALYSES OF ANTIRRHINUM POLLEN

Age	Condition	Percentage of fresh substance	
		Reducing sugar	Sucrose
Days		*Per cent*	*Per cent*
0	Alive	0.40	7.20
11	Alive	0.55	6.80
240	Dead	3.90	1.20
310	Dead	2.10	0.32

These results show a perceptible decrease in the stored sugars as the age of pollen increases, this reserve probably having been used in respiration. As the dead pollen still contained a large amount of stored food, it is improbable that a lack of it had caused the mortality.

Decrease of certain enzymes

Since cane sugar is the chief storage carbohydrate, invertase would be one of the important enzymes present. Tests were therefore made of the activity of invertase as the age of the pollen increased. Weighed quantities (100 milligrams) of Antirrhinum pollen were placed in small bottles at room temperatures. At the intervals given in table 17, invertase was extracted and a determination of its activity was made. The method used was similar to the one recommended by Green (1894). The pollen (100 milligrams) was ground for several minutes in a mortar with a few drops of a 5-per-cent sodium-chloride solution. It was then diluted to 10 cubic centimeters and filtered. To 10 cubic centimeters of 5-per-cent cane-sugar solution was added 2 cubic centimeters of this extract. Digestion continued for twenty-four hours at 30° C. The results are given in table 17.

These results indicate a marked decrease in the invertase content in dead pollen over that in live pollen. However, there is still some invertase present.

TABLE 17. INVERTASE ACTIVITY OF ANTIRRHINUM POLLEN

Age of pollen	Invert sugar	Condition of pollen
Days	*Milligrams*	
0	189.7	Alive
30	195.6	Alive
270	7.7	Dead
570	15.8	Dead

An increase in the proportion of reducing sugar as the age of the pollen increases is shown in table 16. There are several possible explanations of this. A decrease in respiration would tend to result in a surplus of reducing sugar, provided that invertase activity continued at the same rate. In other words, this respiratory material would not be used as rapidly as it would be formed. There may also be a readjustment in the cell protoplasm which would bring more of the enzymes in contact with the cane sugar. As metabolic activities proceed, this reorganization may very probably be taking place.

This suggests the theory of Crocker and Groves (1915) that the death of seeds is caused by a coagulation of the proteins of the protoplast. An attempt was made to apply the temperature-time-of-coagulation formula to loss of viability of Antirrhinum pollen. Consistent results could not be obtained, probably because the moisture content of the pollen grains varied. However, it was found that Antirrhinum pollen can withstand high temperatures to a remarkable degree.

The activity of catalase was very great in fresh pollen. There was some activity in dead pollen, but the decrease over that of fresh pollen was noticeable.

Storage experiments with corn pollen

Since the results of previous workers pointed to the beneficial effects of low moisture conditions on pollen longevity, experiments were made with this in mind, in 1915. Sweet corn was used, the variety being Golden Bantam. Corn pollen for each series was mixed thoroly and stored, in paper envelopes, in covered glass fruit jars. The pollen was divided into several envelopes, for convenience in withdrawing parts of it at the end of each interval. Each jar had several inches of anhydrous

calcium chloride in the bottom. The receptacles were then placed in constant-temperature ovens, at the temperatures noted in tables 18, 19, and 20. At the end of each specified interval, an envelope was withdrawn from each jar, and with its contents field pollinations were made. After a suitable interval, the ears were examined to determine whether fertilization had occurred. Ability to fertilize was the only test of viability used, since uniform results could not be obtained in artificial germination experiments.

In table 18, fertilization is indicated by a plus sign, and lack of fertilization by a minus sign. The number of ears pollinated was either one, two, or three, as indicated by the number preceding the sign.

TABLE 18. CORN POLLEN STORED AT DIFFERENT TEMPERATURES OVER CALCIUM CHLORIDE. 1915

Length of storage	Fertilization when stored at				
	−17° C.	0° C.	12° C.	22° C.	34° C.
Hours					
6	.....	.....	1+	1+	2—
12	.....	.....	1+	.....	.....
22	.....	1+	1+	.....	.....
24	1—	.....	1+	2+	2—
30	1—	.....	.....	1—	2—
32	.....	.....	1+	.....	.....
36	.....	.....	.....	2—	.....
45	.....	1+	1+	.....	.....
48	1—	.....	.....	.....	.....
51	.....	1—	.....	.....	.....
54	1—	.....	.....	3—	2—
60	.....	.....	.....	2—	.....
72	1—	.....	1+	.....	1—
78	.....	.....	.....	.....	1—
94	.....	1—	.....	1—	1—
99	.....	.....	1—	.....	.....
120	1—	1—	.....	.....	.....
131	.....	3—	.....	.....	.....
179	.....	3—	.....	.....	.....
192	1—	.....	.....	.....	.....

These results point to the fact that moderately low temperatures are most favorable for storing corn pollen, provided the humidity is low. It should be noted that pollen stored at a temperature of −17° C. was not capable of effecting fertilization. In this series, no pollinations were made

until after twenty-four hours. There is no evidence as to the exact time at which the loss of fertilizing power occurred.

TABLE 19. CORN POLLEN STORED AT DIFFERENT TEMPERATURES AT A HUMIDITY OF 5–10 PER CENT. 1915

Length of storage	Pollen stored at							
	0° C.		10° C.		20° C.		30° C.	
	Ears pollinated	Fertilization	Ears pollinated	Fertilization	Ears pollinated	Fertilization	Ears pollinated	Fertilization
Hours	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
6	4	0	2	45	1	85	3	90
12	3	0	2	60	2	45	.....	.....
15	4	0	.....	20	.....	.....	2*	45
24	2	0	5	49	4	36	2	3
30	3	0	7	0	2	0	1	0
36	.....	.....	.....	.....	2	30	.....	.....
48	.....	.....	3	0	6	0	.....	.....
54	.....	.....	1	0	1	0	.....	.....
60	.....	.....	3	0	.....	.....	.....	.....
72	.....	.....	4	0	.....	.....	.....	.....

* Pollen adhering.

TABLE 20. CORN POLLEN STORED AT 80–90 PER CENT HUMIDITY AT TEMPERATURES OF 20° C. AND 30° C. 1915

	Length of storage	Ears pollinated	Fertilization
	Hours	*Number*	*Per cent*
Pollen stored at 20° C.	6	2	24
	24	2	67
	30	2	82
	36	2	5
	48	3	23
	54	1	6
Pollen stored at 30° C.	6	1	98
	15	.....	.....
	24*	3	0
	30*	2	0

* Pollen adhering.

In the experiments conducted in the summer of 1916, pollen was subjected to different moisture, as well as different temperature, conditions. The pollen was stored in bottles. The several percentages of moisture were obtained by drawing air thru different concentrations of sulfuric acid, according to the tables of Landolt-Börnstein. Withdrawals and field pollinations were made as in the 1915 experiments. The percentage of fertilization was obtained by actually counting the fertilized and unfertilized ovules on each ear.

TABLE 21. CORN POLLEN STORED AT 30° C. AND 20–30 PER CENT HUMIDITY. 1916

Length of storage	Ears pollinated	Fertilization
Hours	*Number*	*Per cent*
6	1	0
12	3	12
24	2	0
30	2	0

Other storage experiments were made, but temperature conditions at pollination time were so unfavorable that the results were discarded.

Under conditions of high humidity, moisture often collects on the pollen, causing the grains to swell and adhere to one another. On microscopic examination, films of water are seen around the grains. This water does not come from the air, but is excreted by the pollen grains themselves. This is shown by the fact that this " caked " pollen has not increased in weight. As individual pollen grains differ in the amount of colloids and in the concentration of osmotically active substances, it is possible that one grain extracts water from another. However, if this were true, one would expect some grains to be shrunken, which is not the case, so some other explanation must be found. Such changes as coagulation or precipitation of the proteins may take place within the protoplast, which would lessen its power to retain water. A secretion of water would then result. The caking of pollen impairs its viability and interferes with the mechanical operations of pollination. Caked pollen is also a favorable medium for the growth of molds and other fungi.

The results of these experiments again show the favorable effects of fairly low temperatures. A freezing temperature, however, seems to be injurious, and in this respect corn pollen differs from pollen of most species. When corn pollen does not adhere, high humidity seems to prolong its fertilizing power.

Only two storage experiments were conducted in 1917, owing to war conditions. The pollen was stored in watch glasses, over different percentages of sulfuric acid. Novy jars were used. The pollinations were made as in 1916. The results are given in table 22:

TABLE 22. CORN POLLEN STORED AT 6°–10° C. UNDER HUMIDITIES OF 50 PER CENT AND 80 PER CENT. 1917

Length of storage	Ears pollinated		Fertilization	
	50 per cent humidity	80 per cent humidity	50 per cent humidity	80 per cent humidity
Hours				
6	1	3	85	45
10	3	3	48	20
24	2	2	75	52
30	3	3	62	62
46	.....	6	.....	34
54	.....	1	.....	60
71	3	3	70	30

Pollen produced in 1917 was more virile than that of previous years and it is to be regretted that more experiments could not be made. Contrary to the results of the previous year, the lower humidity was the more favorable to longevity.

In order that atmospheric conditions might be more easily controlled, corn plants were grown in the greenhouse in 1919. As a result, favorable and uniform temperatures were maintained both day and night during pollination time, which was a great aid in getting comparable results.

As in previous seasons, actual fertilizing power was the only test of viability used. The method of storage of pollen was the same as in 1917.

The results from these experiments (tables 23, 24, 25) are not very conclusive, altho it can be seen that the pollen lived longer at the lower temperatures. The percentage of fertilization was smallest at the lowest

TABLE 23. CORN POLLEN STORED AT 14° C. AND 70 PER CENT HUMIDITY. 1919

Length of storage	Ears pollinated	Fertilization
Hours	*Number*	*Per cent*
4	2	43
11	1	70
25	1	0
35	2	0
50	2	30
60	1	60
71	1	0
85	1	0
100	2	5
108	0	0
121	4	0

TABLE 24. CORN POLLEN STORED AT 25° C. AND 50 PER CENT HUMIDITY. 1919

Length of storage	Ears pollinated	Fertilization
Hours	*Number*	*Per cent*
5	2	42
24	1	50
32	2	25
46	2	45
58	2	45
72	1	0

TABLE 25. CORN POLLEN STORED AT 11° C. UNDER RELATIVE HUMIDITIES OF 35 PER CENT AND 50 PER CENT. 1919

Length of storage	Ears pollinated		Fertilization	
	35 per cent humidity	50 per cent humidity	35 per cent humidity	50 per cent humidity
Hours	*Number*	*Number*	*Per cent*	*Per cent*
9	2	2	0	20
26	2	2	0	15
34	3	2	5	22
49	2	2	7	0
58	2	2	0	0
72	1	1	15	0
79	1	2	10	7
94	2	.....	.....	.....
100	.....	2	.....	0
109	.....	1	.....	0

humidity. Altho the results of corn-pollen storages are not conclusive, it is justifiable to say that fairly low temperatures (5°–10° C.) are more favorable than high temperatures or temperatures below freezing. Pollen lives longer at moderately high humidities (50–70 per cent) than in a dry atmosphere. However, if the humidity is too high, the pollen becomes sticky. Under the optimum conditions, as stated above, good, virile corn pollen should live for three days. The results show that pollen varies greatly in different seasons, however.

Possible causes of death of corn pollen

Loss of moisture

Andronescu (1915) found that corn pollen lost moisture rapidly when exposed in the open air or in a desiccator. He concluded that death was caused by this drying out. The following experiments were performed to gather additional data. Several grams of fresh corn pollen were spread out evenly on a large watch glass and carefully weighed. The watch glass was then placed in a desiccator and weighings were made as shown in tables 26 and 27. From a similar, but unweighed, sample, adjacent to it, pollinations were made at the same time that the weights were taken.

In a dry atmosphere, corn pollen loses moisture rapidly. Some of this loss in weight is obviously due to the carbon dioxide given off in respiration, but the calculated correction for this loss is only 6 per cent for the figures given in table 26, and 9 per cent for the values in table 27.

TABLE 26. POLLEN IN DESICCATOR OVER CALCIUM CHLORIDE AT 25° C.

Age	Ears pollinated	Fertilization	Water lost
Hours	*Number*	*Per cent*	*Per cent*
0	2	75	0
2	1	60	14
4	1	80	26
6	1	70	37
8	2	40–60	48
10	2	5–65	58
12	2	1–20	79
23	2	0–10	94

TABLE 27. CORN POLLEN IN DESSICATOR AT 25° C. AND 35 PER CENT HUMIDITY

Age	Ears pollinated	Fertilization	Water lost
Hours	*Number*	*Per cent*	*Per cent*
0	1	70	1
2	1	60	12
7	2	36–55	26
10	1	30	43
23	1	1	74

However, pollen remains viable after considerable desiccation. Thus, table 26 shows that fertilization took place even when 88 per cent of the water content had disappeared. In these experiments, the pollen was spread out on the watch glasses in as thin layers as possible, in an attempt to get the same amount of evaporation from each grain. It is probable that the few successful pollinations, after twelve and twenty-three hours, respectively, were due to pollen grains so favorably situated as to hold a larger amount of water. However, the results show that grains may lose from 40 to 50 per cent of their water without materially impairing their viability.

Experiments on respiration

In addition to desiccation, other factors which might impair viability suggested themselves. Since the moisture content of corn pollen is high, respiratory activity would probably be great. As a result, exhaustion of stored food might occur, and this would probably be accompanied by protoplasmic changes.

Respiration was first determined. Due to the small amounts of material available, difficulty was experienced in finding a method by which such small amounts of carbon dioxide could be accurately measured. Truog's (1915) method, as modified by Gurjar (1917), was finally used. This method consists essentially in catching carbon dioxide in a special form of absorption tower, containing standard strength of barium hydroxide, and titrating the remaining alkali against a standard acid. The results are given in table 28.

As was expected, the respiratory activity was high, diminishing rapidly in a dry atmosphere. However, it was not rapid enough to exhaust

TABLE 28. RESPIRATION OF FRESH CORN POLLEN AT A TEMPERATURE OF 25° C.

Time	Weight of pollen	Carbon dioxide per gram per hour
Hours	*Grams*	*Milligrams*
2.5	6	2.11
3.0	6	1.71
3.0	6	0.36

all the stored carbohydrate within the several days that corn pollen normally retains its vitality.

Starch content of pollen

Microchemical tests show corn pollen to consist almost entirely of starch. In dead pollen, there is no apparent diminution in the starch content. Actual chemical analysis, using Sachsse's method, gave the results shown in table 29:

TABLE 29. CARBOHYDRATE ANALYSIS OF CORN POLLEN

Age	Fresh substance	
	Starch	Reducing sugar
	Per cent	*Per cent*
Fresh	15.2	0.23
4 days	13.6	0.46

It is evident, therefore, that the stored food is not exhausted before death occurs.

Amylase activity

Since starch is the chief reserve carbohydrate, amylase must be an important enzyme. Determinations of amylase activity, with both fresh and dead pollen, were made by the following method. A weighed quantity of pollen (0.1 gram) was ground in a mortar with a few drops of distilled water until maceration was complete, after which it was filtered, and 2 cubic centimeters of the extract was added to 10 cubic centimeters

of 1-per-cent soluble starch. After twenty-four hours digestion at 30° C., the reducing sugar was determined. The results showed no decrease in amylase activity of pollen one week old below that of fresh pollen. The amylastic activity of seven-months-old corn pollen showed a marked diminution. This has no significance, however, as corn pollen remains viable for only a few days.

Catalase activity

Catalase activity was also determined. The method of extraction was similar to that for amylase. The Bunzell (1914) apparatus, graduated to read positive pressures, was used. Determinations were made at 25° C. The results (table 30) are the average of five determinations for each age of pollen.

TABLE 30. CATALASE ACTIVITY OF CORN POLLEN

Age of pollen	Reading after 1 minute	Reading after 2 minutes	Reading after 3 minutes	Reading after 4 minutes
Hours	*Millimeters*	*Millimeters*	*Millimeters*	*Millimeters*
6	4.3	7.1	8.7	9.8
38	3.6	5.7	6.9	7.6
58	2.8	5.3	6.2	6.9
106	2.8	5.3	6.2	7.0

As was expected, catalase activity seems to parallel respiratory activity, as was found by Appleman (1916) with the potato; but there is no indication that it has any relation to viability. Dead pollen still shows some catalase activity. Calculated in grams of fresh substance, the catalase activity is much lower than in Antirrhinum pollen.

From these experiments, the author must agree with Andronescu (1915) that the death of corn pollen is normally due to drying out, and not to exhaustion of stored food or to loss of enzymes. This is borne out by the results of the storage experiments, in which the high humidities prolonged life. Nevertheless, the pollen can resist desiccation to a considerable degree without impairing its viability. Even at high humidities, which lessened evaporation, the life of the pollen was not greatly prolonged. Some other factor, such as protein precipitation, may, therefore, be operating.

Resistance of pollen to extremes in temperature

The results obtained by various workers show that pollen is very resistant to low temperatures. It is much less sensitive than the stigma.

Goff (1901) found that plum and cherry pollen germinated after exposure to a temperature of −20° C.; raspberry pollen withstood a temperature of −23° C. Pollen of plum and cherry, confined for five days at a temperature of 20° C. in a saturated atmosphere, failed to germinate, while at 10° C. they germinated freely. Goff concluded from this that if the weather remained cool, a prolonged rainy spell would not be as injurious as at a higher temperature.

Ewert (1911) subjected apricot and peach pollen to a temperature of from −8° to −15° C. for a period of from two to three hours. The results were not uniform, altho high resistance was shown.

Sandsten (1910) found that freezing did not seriously injure apple, pear, and plum pollen, while less than 50 per cent each of the peach and apricot pollen were killed. A temperature of −1° C. caused permanent injury to the stigma of apple, pear, peach, plum, and cherry.

Chandler (1913) determined that apple pollen, when dried, would withstand a temperature as low as from −8° to −13° C. for eighteen hours. At −4° C. apple and cherry stigmas were killed, and of the peach stigmas, 43 per cent were killed at that temperature.

The low water content of Antirrhinum pollen suggests that it possesses considerable resisting power to low temperatures. The success attending the storage at freezing temperature, and even at a temperature of −30° C., led the author to try lower temperatures. Pollen was placed in stoppered test tubes and frozen in liquid air, with the results shown in table 31:

TABLE 31. RESISTANCE OF ANTIRRHINUM POLLEN TO TEMPERATURE OF LIQUID AIR

Time in liquid air (minutes)	5	15	15*	30
Germination (per cent)	60	60	60	60

* After being in an ice-salt mixture for 30 minutes.

The germination was equally vigorous in all treatments, and even longer germ tubes were produced by pollen which had been frozen. The rate of the fall in temperature had no effect. No pollinations were made, but since germination was so vigorous the pollen undoubtedly was able

to effect fertilization. As the temperature of liquid air is somewhere near −180° C., the resistance shown is very remarkable.

Corn pollen is not able to withstand such low temperatures. Andronescu (1915) mentions the stimulative effect on corn-pollen germination of a temperature of from 8° to 14° C. In the storage experiments, there is a record of corn pollen which fertilized after forty five hours storage at 0° C. At −17° C., the pollen was dead after twenty-four hours. It is probable, therefore, that it cannot withstand a temperature much below freezing.

Antirrhinum pollen also is able to resist fairly high temperatures, as is shown by table 32. Other results, not included in the table, were similar.

TABLE 32. ANTIRRHINUM POLLEN STORED AT 52° C.

Time of storage	Germination	Length of germ tubes
Hours	*Per cent*	
11.75	75	Short
12.25	75	Short
12.75	50	Short
13.75	60	Short–medium
14.25	30	Short
14.75	10	Short
15.25	15	Short

Altho germination resulted after storage at this high temperature, it was weak and most of it abnormal in appearance, the germ tubes being short and swelled at the apexes. It is doubtful whether any fertilizations would have resulted from pollinations made with this pollen.

At the time when these experiments were made, the behavior of the pollen subjected to the high temperatures impressed certain facts on the mind of the author. Death seems to be progressive, with no point of absolute distinction between live and dead pollen. Germination became weaker and weaker as the duration of subjection to the higher temperature increased. This germination was abnormal but there was always the uncertainty as to whether the pollen was really alive. Living protoplasm is organized, while dead protoplasm is disorganized. Disorganization cannot occur quickly but must take place in stages, the rapidity being

dependent on the kind and intensity of the adverse condition. While these changes are going on, it is naturally difficult to judge whether or not the protoplasm is viable.

DISCUSSION OF RESULTS

The results of the studies with the pollen of *Antirrhinum majus* (snapdragon) and of *Zea Mays* (corn) show the striking dissimilarities between them. In the pollen of Antirrhinum, metabolic activity is weaker than in the corn pollen, as evidenced by less respiration, lower water content, and greater ability to withstand extremes in temperature. It would seem that the factors influencing longevity of Antirrhinum pollen are the same as in certain kinds of seeds. Desiccation, exhaustion of stored foods, and decrease of essential enzymes do not appear to be important. These same factors have not been found to be important in the loss of vitality of the seeds. Altho the author has no data to substantiate this, the theory of Crocker and Groves (1915) that death is caused by slow precipitation of proteins within the protoplasm, seems to be the most logical. The increase in reducing sugars, with increasing age, is evidence in favor of this theory, for it shows that some readjustment is taking place.

When corn pollen is subjected to normal atmospheric conditions, drying out undoubtedly determines the duration of vitality. When stored under conditions of high humidity, however, the vitality is not greatly prolonged. Altho respiratory activity is great, no marked loss of reserve materials occurs. As with Antirrhinum pollen, some destructive change must be going on within the protoplast. A change in the protoplasmic emulsion, such as precipitation, would affect the imbibitory powers of the colloids and might cause the excretion of water noted in the experiments.

With pollen, one must distinguish two degrees of vitality, one which can bring about germination and short tube growth, and another which will cause fertilization to take place. The author has given considerable evidence in these experiments that a pollen grain may germinate without ever functioning in fertilization. It is an open question whether this is due merely to the inability of the pollen tube to reach the ovary. Pollination experiments, under favorable temperatures, on short styles or styles of which the major parts have been severed, with a study of tube growth within the style, would shed some light on this.

The results from the storage experiments with pollen were exceedingly variable. Many factors that are difficult to control may influence the results. Pollen produced in different seasons and under diverse conditions is, in some way, physiologically different, as is shown by the differences in water content, the different optimum sugar concentrations required for germination, and the variations in the duration of life. Temperatures at pollination time, especially if unfavorable, may also influence results. It is an established horticultural fact that a larger "set" of fruit occurs on "selfed" varieties in seasons when the temperatures are most favorable for pollen tube growth. In the corn-storage experiments, where field experiments were made, it was, of course, impossible to control the temperature. In the Antirrhinum-pollen-storage experiments, all plants were grown in the greenhouse, so this factor was probably negligible.

The difference in resistance of the two kinds of pollen to extremes of temperature was striking, altho it was about what one would expect. Corn pollen with a high water content and high respiratory activity was more susceptible to injury than was Antirrhinum pollen with its low water content and weak respiratory activity. If death is due to an irreversible change of the protoplasmic system, a protoplasm like that of Antirrhinum pollen would be more resistant because of its low water content and, consequently, more stable, gel-like emulsion.

According to Harvey (1918), in addition to water content and metabolic activity, the basicity of the protoplasm also influences the resistance to low temperatures. In these studies, no hydrogen-ion determinations of pollen protoplasm were made.

SUMMARY

Pollen of snapdragon (*Antirrhinum majus* L.) germinates in any concentration of cane sugar up to 30 per cent. The most favorable concentration varies from 10 to 25 per cent, depending on the conditions under which the plant has been grown.

The most favorable temperature for the germination of Antirrhinum pollen is about 25° C.

The moisture content of Antirrhinum pollen varies from 10 to 20 per cent.

Cane sugar is the chief reserve carbohydrate in Antirrhinum pollen, the amount ranging from 8 to 10 per cent of the fresh substance.

Antirrhinum pollen remains viable longest under conditions of low temperature (0° to −17° C.). The longevity decreased when pollen was stored in oxygen or at reduced atmospheric pressures. There is some evidence that high percentages of carbon dioxide in the atmosphere favor longevity. The maximum duration of germinative ability was 670 days, and of fertilizing power 161 days.

The death of Antirrhinum pollen is not due to desiccation, exhaustion of stored food, or weakening of essential enzymes.

Antirrhinum pollen is extraordinarily resistant to extremes of temperature, being able to withstand one as low as −180° C. and one as high as +52° C.

Corn pollen is difficult to germinate. The optimum concentration for germination varied, depending on the conditions under which the plant had been grown. The best germination resulted in a 15-per-cent cane-sugar solution plus 0.7-per-cent agar.

The moisture content of corn pollen was between 50 and 60 per cent, depending on the conditions under which the plants had been grown.

The chief reserve carbohydrate in corn pollen is starch. Analyses showed that about 15 per cent, expressed in percentage of fresh substance, was present.

Corn pollen remained viable longest under conditions of moderately low temperature (5° to 10° C.) and moderately high humidities (50 to 80 per cent). This pollen was killed at a temperature of −17° C. The maximum duration of retention of fertilizing power was from seventy to eighty hours.

Under normal conditions, the death of corn pollen is caused by desiccation. However, since life is not greatly prolonged by storage under conditions which retard evaporation, moisture is not the only important factor.

Pollen may germinate in an artificial medium and yet be incapable of fertilizing a flower.

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HORSE RAISING IN COLONIAL NEW ENGLAND

DEANE PHILLIPS

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CONTENTS

HORSE RAISING IN COLONIAL NEW ENGLAND

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DEANE PHILLIPS

With the rapid rise of the sugar industry in the West Indies during the latter half of the seventeenth century, the continental British colonies in America were called upon to serve as the main source of supplies for the sugar plantations. An important trade grew up, especially with the New England region, in which the islands received lumber, fish, foodstuffs of various sorts, cattle, and horses. In return the northern colonies obtained sugar, molasses, rum, dyestuffs, and — of especial importance to New England — specie in various forms which could be used for purchasing manufactured articles and other needed supplies from England.

Horses were used on the sugar plantations to turn the rollers of the cane-crushing mills, to haul the cane from the fields, and to transport sugar and supplies. They were in demand for saddle purposes also. As far as New England was concerned, there is ample evidence that the exportation of horses to supply this need of the sugar islands formed a very important part of the commerce which was carried on between the two groups of British colonies in the New World, and that it was equally important in the trade which grew up between New England and the French West Indies when these islands also began the cultivation of sugar. The observations of contemporary writers, the reports of the various colonial governors to the Board of Trade in London, port records and various commercial statistics of the period which have been made available by modern research, and many other scattered sources of information, indicate that this was the case.

It is apparent that the development of such an export trade in horses must have stimulated a corresponding development of horse raising on a commercial scale. In this memoir an attempt has been made to gather together such widely scattered data as are available concerning this early agricultural enterprise of New England, and to trace its development and extent during the colonial period. Since, from its nature, this raising of horses was intimately bound up with the sugar

trade of the West Indies, it has seemed advisable to give some attention also to the growth and development of the latter industry.

SOURCE AND EARLY DEVELOPMENT OF NEW ENGLAND HORSES

It is not at all certain that to the early colonists New England appeared as stern and inhospitable a shore as we are sometimes led to believe. Hardships there were in plenty, and much real privation and want, but, on the other hand, the country gave to them bountifully in many ways of its own. Not the least of its advantages in the eyes of the first settlers was the comparative abundance of pasture and grasses suitable for hay, which assured an easy support for livestock in numbers sufficient for the colonists' needs.

This feature of the country is frequently mentioned in letters written to friends in England by the early settlers and in the accounts of travelers. Thus the Reverend Mr. Higginson (1),[1] writing in 1629, describes the abundance of grass "which groweth everywhere, both verie thicke, verie longe, and verie high in divers places"; and in regard to livestock he records further, "it do prosper and like well this countrie." Another writer (2), possibly too ardent in his admiration for the new land, compares the abundance of pasturage to "Hungaria." Josselyn (3), in his visits to New England, also seems to have been impressed with its possibilities along this line, and writes in 1675 of the "broad vallies supplied with ample forage as well as that to be found in clearings in the forests."

The native grasses which furnished this forage were mainly of two sorts — foul-meadow grass and herd-grass, or timothy (4). English grasses were introduced at an early date and were found to grow well in the new land (5). Both the native grasses made good hay, and this fact rendered it possible to keep livestock with little difficulty in spite of the rigors of the New England winters. The colonists were thus enabled to increase freely the number of their cattle and horses in proportion as they found them useful. As is shown later, they did not fail to avail themselves of this opportunity, and the increase that took place was a rapid one.

[1] Numbers in parenthesis refer to the list of citations beginning on page 930. The sources cited are given in full in the list beginning on page 936.

USEFULNESS OF HORSES TO THE COLONISTS

Cattle and horses were of service to the colonists in many ways. The neat cattle furnished them food, hides for leather, and oxen for draft purposes. Sheep were valued chiefly for wool. Horses served to some extent for draft, but for ploughing and other heavy work they were found less serviceable than oxen. Their most important use was to furnish means of rapid transportation from place to place. In the earliest days of the settlements most of this travel was on foot or in small boats (6), but by 1652 a New England writer (7) could boast of the "wild and uncouth woods filled with frequented ways and rivers overlaid with bridges passable for both horse and foot." This indicates in a general way the transition that soon took place, so that horses became of steadily increasing importance as the settlement of the country proceeded and the towns became more numerous and widely separated.

In the difficulties with the Indians, horses were of especial advantage to the colonists. Not only was this true in the case of offensive operations against the savages, but in the frontier troubles which were always imminent the possession of horses enabled the settlers to bring aid quickly to one another when attacked and thus saved many an isolated settlement from extinction. That the colonists realized this advantage is apparent from the pains which they took to prevent any horses from coming into the hands of the natives. In Plymouth (8), in Massachusetts Bay (9), and in Connecticut (10), laws were passed to prevent the selling of any horses to the natives, and even as late as 1665 it was only after considerable debate that the Plymouth court allowed one such sale to be made to a friendly Indian for purposes of "husbandry" (11).

Lastly, it is interesting to note that horse racing was not unknown even in the early days of the Puritan settlement in the Massachusetts Bay colony, where the court vents its dire condemnation on "certain euill and disordered persons" who engaged in such a breach of public decorum (12). At a later date, however, such racing came to be a recognized sport in Boston (13), and especially in Rhode Island, where races were very common and often for high stakes (14). These practices were not frequent in the early days, however, and came to be

tolerated only after the country was well settled and customs had changed considerably.

EARLY IMPORTATIONS

The first colonists who settled at Plymouth in 1620 brought neither horses nor cattle with them to the new land, and it was not until four years later that the first neat was brought over (15). In the same year the correspondence of Governor Bradford indicates that " a bull and 3 or 4 jades " were to be shipped to him from London to be sold in the colony (16). The first record of the actual presence of a horse in Plymouth seems to be in 1632. Governor John Winthrop, of the Massachusetts Bay colony, describes in his diary a journey made to Plymouth in that year, partly by boat and partly on foot, and states that on his return he was sent a part of the way on " the Governor's mare " as a mark of special respect (17).

However, from some source — probably England, but possibly Holland, with whose ships the colonists had traded (18) — the Plymouth settlers had by 1632 obtained a considerable supply of cattle, for it is stated by Governor Bradford that by this date many persons had been enriched by selling corn and cattle at high prices to newcomers in both Plymouth and Massachusetts Bay and had " spread out on farmes " for the purpose of raising more (19). As to the number of horses in Plymouth at that time, however, no information can be gleaned from Bradford's narrative, for he, in common with other writers of the period, uses the term *cattle* more or less indiscriminately to cover any sort of livestock, including horses.

The richer Massachusetts Bay colony seems to have been better supplied than the colony at Plymouth. The fleet that arrived with its numerous settlers in the year 1629 brought over also a considerable number of horses and cattle, one hundred and fifteen head in all (20), among which were thirteen horses (21). In the following year the ships that brought over Governor Winthrop and the second group of colonists had on board two hundred and forty cows and about sixty horses, as is learned from Winthrop's letters (22). Some of these animals died while *en route* and it is not certain just how many were added to the stock of the colony, but among the horses that survived there were both mares and stallions (23).

After the arrival of these early settlers, the succeeding decade saw the landing of a steady stream of new colonists about the bay. It is reasonable to suppose that they also brought many horses, but specific references to such importations are not frequent. Sir Ferdinand Gorges in 1632 wrote from England to Captain John Mason in Massachusetts promising to send over several at the first opportunity (24), but no mention is made of their arrival. Winthrop also records a few importations, but in a casual and incidental fashion which implies that his register makes no attempt at completeness in this respect. Of those noted by Winthrop, the first is in 1633, when he mentions the arrival of the ship *Bird* with four mares on board (25), and in the same year the *Bonaventure* with two, four having been lost in transit (26). In 1635 Winthrop speaks also of the arrival of a Dutch vessel with " 27 Flanders mares ..... and 3 horses " (27). This last-named ship had cleared at the Texel five weeks previously, and had thus made an unusually quick voyage and one notable for the fact that none of her cargo of livestock had been lost *en route*.

During these early years, also, both Winthrop and Bradford record in their journals the frequent arrival in the bay of ships having cattle on board, and it is probable, for reasons already given, that these " cattle " often included some horses. The number of such arrivals was certainly large. Winthrop, for example, notes that in 1634, " during the week the court was in session there came in six ships with store of passengers and cattle " (28). In the same year there were fourteen ships in one month which cast anchor either in Salem or in Boston (29). Many more arrivals probably went entirely unrecorded, and therefore the scantiness of the record does not necessarily mean that horses were not being brought into the country in considerable quantities. That they were being imported in large numbers is, in fact, the only possible conclusion to be drawn in view of their great abundance a few years later — to confirm which there is plenty of evidence, as will be shown presently.

SOURCES OF NEW ENGLAND HORSES

Since the early importations undoubtedly furnished the basic stock from which two noted American breeds — the Narragansett pacers and the still more famous Morgans — were later developed, it is worth while

to consider briefly the sources and the general characteristics of these first imported horses.

In view of the lack of any direct evidence to the contrary, it is fair to assume that the first shipments were mainly from England and of the small nondescript type which at that time made up the bulk of the English horses (30). There was, however, some admixture of other blood. In the primary importation into the Massachusetts Bay colony in 1629, three at least are mentioned specifically as " having come out of Leicestershire " (31), which at that time was the source of a more or less distinct type of horse of a sort better than the average (32). The importation of Flemish mares also has been noted. Wallace contends that these latter were not Flemish but were rather of a Dutch type (33), but his conclusion is based merely on the fact that the vessel cleared from a Dutch port — which does not seem a very valid reason for controverting Winthrop's specific statement as to their Flemish origin, especially since Flemish horses were well known at that period as a distinct type.

There is one other possible source of some of the New England horses which deserves consideration, especially because it may tend to explain in some measure the persistently small size of these horses, even when carefully bred — as later they were in Rhode Island and Connecticut — and, further, the constant occurrence among them of individuals possessed of a natural pacing gait. This possible progenitor is to be found in the Irish hobbies, a race of small, hardy, wild ponies existing in Ireland during the first part of the seventeenth century. These horses were in great demand in England for saddle purposes, and were exported thence in such quantities that they are said to have become practically extinct in Ireland before the year 1634 (34). They were well known in England, and their natural pacing gait made them especially desirable in any place where travel was of necessity on horseback (35) ; it is not at all improbable, therefore, that some of them found their way to New England, where they would have been especially serviceable. There seems to be no direct evidence to this effect, but any comparison of such fragmentary descriptions of the two as are available discloses a rather striking similarity between these Irish hobbies and

the famous Narragansett pacers which were later developed in Rhode Island.[2]

FREE RANGE AND ITS EFFECTS

From the very earliest period of New England history it was customary to allow both horses and cattle to run at large on the public commons. At times some provision for a herdsman was made, but as the herds increased in numbers and the settlements became more scattered the animals began to roam more or less at will about the settled areas and often strayed away for considerable distances into the forest or were lost completely. Winthrop records a happening of this sort in a letter written to Governor Endicott on behalf of a widow whose horse had been impressed for military service. Pleading her need for the one that had been taken from her, he says, " She hath another horse but has not seen him for several months " (36). Strays of this sort were numerous and this often led to many difficulties of ownership, which in time compelled definite legislative provisions to be made.

Where horse raising developed, as it did later, on the islands of Long Island Sound and on the water-guarded points and necks of Rhode Island, this free range was not a serious problem. But where the horses and cattle were running loose about the towns in a semi-wild state and in ever-increasing numbers, many difficulties were bound to arise. The chief trouble came from damage done to gardens and crops by herds of these equine and bovine marauders. At first " all greate cattle " were herded by day by a public herdsman, and the owners were held responsible for any harm inflicted by their animals after nightfall (37). But soon the burden was put on the other side, and in Massachusetts Bay, for example, in 1642 the court repealed the former act and provided that " every man must now secure his own corn and meadow against damage " (38). It was provided further that only in case animals running at large had broken through an admittedly strong fence could the person suffering the damage have any redress. Complaints for damages of this sort appear continually in the court records of all the colonies, and it was apparently a cause of endless litigation, which persisted until a late date.

[2] A more detailed discussion of the origin of the Narragansett pacers is given on page 922.

Another difficulty met with as a result of open-range conditions was that of deterioration of the breed. Whatever may have been the source of the New England horses, it is clear that the promiscuous breeding of the semi-wild animals on the commons could not be conducive to the perpetuation of their best characteristics, although it may have resulted in a certain hardiness by weeding out the ones unable to stand the rigors of this wild life. At any rate, efforts were made before long to prevent the breeding of the obviously unfit. In 1668 the court in Massachusetts Bay declared: "Whereas, the breed of horses is utterly spoyled whereby that useful creature will become a burden..... be it enacted that no stone horse above two years old be allowed on the commons or at liberty unless he be of comely proportions and fourteen hands in stature" (39). The owner of a horse found in violation of this statute was to be fined, and later the amount of the fine was raised. Plymouth (40) and Connecticut (41) passed similar limitations, the minimum stature in the latter case being set at thirteen hands. These restrictions seem to have been fairly well enforced but could obviously result in little improvement of the breed as long as complete open-range conditions prevailed.

One of the perplexities in all these cases of damages, after horses and cattle had become numerous, was for the person whose premises had been invaded to recognize whose animal it was that had done the damage. The same difficulty was met with in fixing the fines for undersized stallions found running at large. Often these horses and cattle were even strays from a neighboring town, which made the problem still more complicated. This led to the passage of acts compelling the branding of all animals with both the mark of the private owner and that of the town of his residence. The general court in Massachusetts Bay passed such an act in 1647, and in its records are enumerated the marks of thirty-three different towns under its jurisdiction at the time (42). In 1656 the New Haven colony compelled horses to be branded (43), and the other Connecticut towns did the same in 1665 (44). Rhode Island had a similar provision (45). In the latter plantation in 1686, thirty wild and unmarked horses were ordered caught and sold and the proceeds employed to build a prison and stocks (46). This was the usual fate of unbranded animals or persistent strays. In 1661 the court at Plymouth, "on complaint of some that certain horses or horse-

kind belonging to Rhode Island are found goeing within our libertys.... to the great annoyance of Indians and English," ordered that such animals should be treated as common strays and sold (47).

INCREASE IN NUMBER OF HORSES

In the two or three decades following the first importations there was a rapid increase in the number of horses in New England, and they became abundant not only in the region about Massachusetts Bay but also in the newer settlements in Connecticut and Rhode Island. As the colonists pushed into these latter areas they took horses and cattle with them from the earlier settlements, and, finding the new regions in some places especially suitable for the raising of livestock, they began to engage in it on a considerable scale, so that by 1650 or soon afterward there had come about an abundance of both horses and cattle through the whole New England territory.

The increase which thus took place is brought out clearly by the course of prices during the period. In the years of the great immigration that followed the first settlements on Massachusetts Bay, these prices were rather high. Winthrop, in 1633, rates mares as being worth £35, and cows from £20 to £26 (48). Two years later the Flanders mares, the importation of which has already been noted, sold for £34, and heifers brought in by the same ship sold for £12 each (49). During the next few years the great number of settlers arriving caused prices to rise even higher, and, as Bradford records, "ye anciente planters which had any stock begane to grow in their estats and spread out on farmes to raise more" (50).

By 1640, however, the supply had apparently overtaken the demand and prices began to fall (51). By 1645 this decrease had gone so far that Winthrop speaks of a horse the price of which he gives as £10 as a "costlie horse" (52). In 1653, however, horses were still rated by the Massachusetts Bay court at £16 (53), but thirteen years later, in Connecticut, they had fallen to half that amount (54), and in 1668 the Massachusetts Bay court reduced the rate from £10 to £5 (55). Finally, in 1677, the rate was still further reduced in Massachusetts Bay, and horses were ordered to be received at a rate of £3 for each horse or mare above three years old and 40 shillings for two-year-olds (56). In

the last-named case the court stated specifically as its reason for the reduction that horses had for some time been worth much less than the amount previously fixed by law. During this period of falling prices, the number of persons in the country had steadily increased, roads were being established, and new agricultural lands had been opened up — all of which would result in an increased demand for horses. It appears, therefore, that the increase in their numbers must have more than kept pace with the development of the country, and that the decrease in prices was due to the abundance of the supply rather than to any decreased need for their services.

There is much other evidence to indicate that by the middle of the seventeenth century horses had become very abundant. In 1647 those running wild in Massachusetts Bay were so numerous and were doing so much damage as to call for legislative interference (57), while Maverick, writing a little more than ten years later, says, " it is a wonder to see the great herds of cattle ..... and the great number of horses besides the many sent to Barbadoes and the other Carribee islands " (58). The same condition is attested by John Winthrop the younger, writing from Connecticut in 1660 (59), and by the report of the Commissioners to New England presented to the Board of Trade in London in 1665 (60). By 1675, according to William Harris, who had been sent out by the Board of Trade, the country had so many horses " that men know not what to do with them " (61).

A still further indication of the plentiful supply of horses in New England is the fact that by this time these colonies had begun as a source of supply for other colonies. In 1642 Massachusetts Bay was being called upon to furnish a shipment of horses to Lord Baltimore's colony in Maryland (62), and in the report to the Board of Trade in 1665, already mentioned, horses are named as one of the exports of Massachusetts to Barbados and Virginia. A letter written in 1650 by Secretary von Tienhoven, of the Dutch West India Company, indicates that at that date horses were being obtained from New England by the Dutch on the Hudson River (63). The letter in question advises prospective settlers in the New Netherlands to take no horses with them to the new land, because " they can be got at reasonable expense from the English who have plenty of them." There is appended also a

table of prices in " New England " for horses, cows, and hogs; so there can be no doubt as to which of the English settlements Von Tienhoven had in mind.

It is thus apparent that by about the middle of the century or a little later, New England had come to have an abundance of horses more than sufficient for its own needs. Natural increase under free-range conditions would account for such large numbers only if it were assumed that the importations during the early years of settlement were far more numerous than have been recorded, or else that such importations continued throughout the whole period — which does not seem very probable. During the latter part of the years described, however, the exportation of horses, which was just beginning, had as a result the stimulation of horse breeding for this purpose in a more careful manner, and probably accelerated to some extent the rate of increase.

With the development of this export trade begins the second phase of horse raising in New England, resulting in many changes throughout the area and in the establishment of horse breeding as an important and extensive industry in certain favorably located sections.

THE BEGINNING OF THE EXPORT TRADE IN HORSES

As has already been indicated, some horses were exported from New England to the other continental colonies at an early date. Such shipments, however, never came to be of any great importance, and are worthy of mention chiefly to show the relative abundance of horses in New England as compared with their numbers in the neighboring colonies. The main demand that resulted in the exportation of New England horses came from the sugar plantations in the West Indies, where both horses and cattle were needed for draft purposes, to haul the cane from the fields, to transport sugar and supplies, and to turn the heavy cylinders in the cane-crushing mills.[3] Horses were used for

[3] Oldmixon (*The British Empire in America*, vol. 2, p. 147) gives the following description of the operation of these cane-crushing mills: " They grind the canes thus in the cattle mills; The Horses and Cattle being put to the tackle, go about, and turn by sweeps the middle Roller; which being cogged to turn others at the upper end, turn them about. They all three turn upon the same centers which are of Brass and Steel, going so easily of themselves, that a Man, taking hold of one of the Sweeps with his Hand, may turn all the rollers about; but when the canes are put between the rollers it is a good Draught for five Oxen or Horses."

saddle purposes also by the sugar planters, who were willing to pay high prices for superior animals of this type.

That the New England colonies, rather than any of the other continental settlements, should have become the accepted source of supply for this demand from the sugar islands, resulted chiefly from the fact that they were the only ones which possessed a surplus of horses at the time when the demand first began to make itself felt, about the middle of the seventeenth century. In most of the other colonies there was an actual scarcity of horses, as in Virginia (64). The Dutch in New Netherlands, it is true, did actually export some horses during the year 1650, but an act was soon passed which forbade such shipments (65). It thus came about that in the early days of the sugar industry in the West Indies, New England had no real competitor among the continental colonies in supplying the growing demand for horses for the sugar plantations. Virginia furnished many cattle (66), and after 1700 the colony on the Hudson River, by that time in English hands, again began the shipment of horses; but New England's leadership in the trade was never seriously threatened during the colonial period.

The continental American colonies proved to be a convenient source of supply to the sugar islands of the West Indies, not only for horses and cattle but for many other commodities as well. The trade in horses, in short, was an integral part of the much more extensive commerce which grew up between the West Indies and the northern British colonies whereby the islands were supplied with timber, boards, staves, fish, and provisions of all sorts, in return for sugar, molasses, rum, dyestuffs, and, most desirable of all, Spanish dollars and bills of exchange on London. The extent of the export trade in horses at any particular period, therefore, was influenced by the condition of this commerce as a whole and by the changes that took place in the sugar industry itself. Wars, acts of Parliament, competition between the Islands — in short, all factors that aided, hindered, or changed the direction of this larger trade — had their effect on the exportation of horses. Certain changes in the manufacture of sugar which took place during the first part of the eighteenth century also tended to decrease the demand for horses. Since, therefore, the horse raising that developed in New England during the later part of the colonial period was essentially dependent on

this export trade, it is necessary in any further treatment of the subject to consider in some detail the rise and development of the sugar industry itself.

RISE OF THE SUGAR INDUSTRY IN THE BRITISH WEST INDIES

At the beginning of the seventeenth century, Europe was being supplied with sugar mainly by the Portuguese, from Madeira and, more especially, from their settlements on the mainland of South America, in Brazil. The English also had probably produced some sugar in South America, from Surinam, before ceding that colony to the Dutch by the treaty of Breda (67), but it was not until they had established a settlement in Barbados, one of the Windward Islands, that they began to be serious competitors of the Portuguese.

The colony in Barbados had been settled for some time before 1630, but for a considerable period it had produced only indigo, ginger, cotton, and "bad tobacco," which brought in but moderate returns. Sugar culture was introduced in or about the year 1642, and by 1650 the planters had grown proficient in its production and were shipping it to England in considerable quantities (68). The new industry met with remarkable success and within a few years the island had become very prosperous; lands had increased greatly in value, and the planters had amassed great wealth and were found living on a scale of surprising pomp and luxury. In 1661 King Charles II created thirteen baronets from among these planters, none of whom are said to have had an annual income of less than £1000 and some of whom had more than £10,000 a year. In the same year the trade of the island is estimated to have supported more than four hundred ships and the value of the exports is placed as high as £300,000 (69).

The great success of Barbados stimulated the growing of sugar on the other islands of the British West Indies. St. Christopher (which the English shared with the French), Nevis, Montserrat, Antigua, and lastly, after its capture from the Spanish in 1655, Jamaica, all came into the market with sugars and the trade grew at a rapid rate. The Navigation Acts, confining this commerce to British bottoms, soon made London the chief sugar mart of the world, whence the product was re-exported by British merchants. English sugars undersold those of

the Portuguese, and by 1670 the latter had been forced out of practically all the markets north of Cape Finisterre (70).

EARLY EXPORTATION OF NEW ENGLAND HORSES

The rapid development of the British sugar islands called for great quantities of supplies to carry on the work of the plantations, and, since the islands had few resources of their own, importations were necessary. Provisions from Ireland, slaves from Africa, shoes and other manufactured goods from Europe, as well as the products of the continental British colonies — the nature of which has already been indicated — all were brought into the islands, and of these supplies horses were a not unimportant item.

In the earliest days of the sugar industry, trade was still free and the Dutch and the Portuguese seem to have furnished the British islands with as many horses as were needed (71). With the stoppage of this trade by law and the increasing development of the plantations, however, recourse was had to England and to New England to supply the demand. During the period between 1649 and 1658 the importations of English horses were especially numerous. In those years there are recorded in the British Colonial Papers forty-eight different permits for such shipments, for a total of more than nineteen hundred horses (72). England continued to send horses until as late as 1667 (73), but the levying in 1654 of an export duty of 20 shillings a head (74) cut down the numbers considerably and hastened the shift in the trade by which New England at length became almost the sole source of supply for the islands. In that region there was no export duty except in Massachusetts Bay, where it was only sixpence, and the cost of transportation was much less because of the shorter distance, which resulted also in much smaller losses in transit.

The trade of Massachusetts Bay with the West Indies had already been established before the production of sugar in the British islands had come to be of importance, and so it is only natural that with the rise of the latter industry and the demand for horses the growing surplus of New England animals should receive the advantage of the outlet thus opened. As a result, horses were being shipped from Massachusetts ports fully as early as from those of England, and, for

the reasons given, the numbers exported soon exceeded those from the English ports. Concerning the beginning of this trade Winthrop writes in 1647: "It pleased the Lord to open to us a trade with Barbados and the other islands . . . which as it proved gainful, so the commodities which we had in exchange for our cattle and provisions, as sugar, cotton, tobacco, and indico were a good help to discharge our engagements with England" (75).

As to whether there were any horses among these "cattle" which Winthrop states were being sent to the West Indies, there is no evidence. The record of such exports is, in fact, much like that of the early imports into the country, and specific mention of such shipments is not frequent, even though more general statements, such as those to be found in the reports to the Board of Trade in London, indicate that they were taking place. In 1648 Winthrop notes in his journal the presence of a ship "lying before Charlestown with eighty horses on board bound for Barbadoes" (76), and this is probably the first recorded exportation of horses from New England to the West Indies. Wallace states (77) that there was a shipment of eighty head in 1640, but he does not give the source of his information and it is more than probable that it is this exportation of 1648 to which he refers, inasmuch as the demand for horses had hardly begun in Barbados as early as 1640.

The exportation of horses from New England in 1648 or before was evidently not limited to this one cargo, however, for a writer who styles himself Beauchamp Plantagenet, describing a visit to Barbados in that year, states that "New England sendeth horses and Virginia oxen" to turn the sugar mills in the island (78). In 1649 the Massachusetts Bay court passed an act forbidding the exportation of mares and placing a tax of sixpence on every gelding sent out of the country (79). This was obviously an effort in the main to protect the breeding stock of the area, and Massachusetts Bay urged that similar prohibitions be adopted by all the United Colonies of New England. The colony at New Haven was the only one to act on the recommendation (80), and in Plymouth and Rhode Island there continued to be no restriction on such shipments. That such a law was found desirable in Massachusetts was due partly to military considerations, but the fact serves also as

an interesting side light on the extent of the demand for horses, for it is clear that at that time there was no great scarcity of them in the region.

The trade between Massachusetts Bay and Barbados was more or less interrupted during the period of the Commonwealth in England, as a result of the refusal of Barbados to submit to the new authority; but, in general, the exportation of horses from the colony continued on a considerable scale, and there is much evidence of the growing dependence of the islands on the New England region as a source of supply. The report of the Commissioners for New England to the Board of Trade in London in 1665 states that Massachusetts exported fish, pork, beef, horses, and corn to Virginia and Barbados (81). Inasmuch as horses are not mentioned as a product of any of the other colonies, in the report, it may be inferred that the region about Massachusetts Bay was still the chief source of supply among the continental colonies. In 1673 Captain Gorges was instructed by the Assembly of Barbados to insist to the English Parliament on the dependence of the island on New England for " boards, timber, pipe staves, and horses," to the end that no acts might be passed which would interfere with the trade (82). And in 1675 a certain " Mr. Harris of New England " gave an account of the trade of the country, in which he says that " to Barbadoes in exchange for horses, beef, pork, butter, cheese, flour, peas, biscuit, we have sugar and indigo " (83).

In 1700 Massachusetts Bay was still sending large numbers of horses to Barbados, and also to the Leeward Islands and to Jamaica. Toward the end of the century, however, many of the horses shipped were animals that had been raised farther inland and had been driven considerable distances to be sent out from the ports on Massachusetts Bay (84). This is shown, for example, by the correspondence of Waite Winthrop with his brother Fitz-John, of Connecticut, by which it appears that the latter was sending horses overland to Boston from his plantation on Fisher's Island, in Long Island Sound (85). There was thus taking place a shift in the raising of horses in New England, by which other regions than that about Massachusetts Bay were coming to be of increasing importance, especially as regarded the export trade.

As the settlement of New England proceeded, it was very soon dis-

covered that there were certain areas in Rhode Island and in Connecticut which were much better adapted to the raising of livestock of all kinds than the region first settled (86). These more favored areas were found mainly in the upper valley of the Connecticut River, along the shore of Long Island Sound, and about Narragansett Bay in Rhode Island. Here plenty of level, well-watered pasture lands were found, swamp grasses which made good hay were abundant, and in many places the grazing areas were intersected with salt-water ponds and lagoons which served to separate pasture land from cornfields far more effectively than any fence could have done. The damages and endless difficulties resulting from free range in other less favored sections made this last-named feature one of no mean advantage in the raising of livestock and in the improvement of the breed. The few cattle, sheep, and horses which the first settlers in these regions brought with them were soon augmented by others, and before long the obvious agricultural advantages of the new areas were being used to their full extent.

With the coming of the demand for shipment to the West Indies, horses and cattle were soon being raised for export in these more favored districts. Some horses were apparently being shipped from Newport as early as 1656, but there is some question as to whether this particular shipment did not consist of horses stolen from Massachusetts instead of animals raised on Narragansett Bay (87). In 1677, however, Captain John Hull wrote to one of his partners in the Pettiquamscut Purchase in Rhode Island, proposing to build a stone wall across Point Judith Neck, "so that no mongrel breed might come among them," and to raise a breed of "large and fair horses and mares" for shipment to the West Indies (88). This plan appears to have been put in operation, for not long afterward Hull wrote to a resident of the district, a certain William Hefferman, accusing him of stealing horses and rather tartly offering to give him some horses that he might have no further need to indulge in such practices (89). By 1680 horses were being shipped from Rhode Island in sufficient quantities to be mentioned by Governor Sanford in his reply to the inquiries sent out by the Lords of Trade and Plantations, in which he states that "the princi-

pal matters which are exported among us is horses and provisions" (90).

In Connecticut, also, horses soon came to be a recognized commodity of trade. From the towns on the upper Connecticut River, as late as 1680 many horses were being driven overland to Boston to be sold, presumably for the export trade (91). The coast region of Connecticut had before this time begun a direct trade with the West Indies. In 1667 it is recorded that a vessel had been sent out from New London bound for the island of Nevis, from which twenty-six horses were lost overboard in a storm (92). Such other evidence as is available indicates that this was not an isolated shipment from New London. This port was, in fact, so situated as to draw not only on a fairly well-adapted livestock area in Connecticut, but also on the most important part of the Rhode Island area, and with the development that continued to take place it in time became the chief center for the exportation of horses from New England. In the period before 1700, however, New London had but made a beginning in this trade, and this was also the condition of Newport, Providence, and the river towns of Connecticut.

HORSE STEALING

One further development took place during the period just described, which casts an interesting side light on the extent of the export trade in horses and its effect on the New England region. This was the growing prevalence of horse stealing throughout all the colonies. One of the objects of the branding of horses and cattle, already described, was to prevent this practice. The brander in most of the towns was a dignitary of no small importance, and as a rule was required not only to brand each animal but also to keep a record of the operation in an official book together with a description of all the natural and artificial marks on the animal and the name and residence of the owner. In Rhode Island (93) and in Connecticut (94) there were fixed severe penalties for any person who took or attempted to take out of the town any horses or cattle without first informing the official brander and receiving his permission.

Branding alone, however, did not provide a very effective check on the stealing of horses and cattle. As the exportations grew in volume and more and more ports were engaged in the trade, it became increas-

ingly easy to conceal such thefts and the practice became surprisingly prevalent. Miss Caulkins, in her *History of New London* (95), has described as follows the conditions during this period:

> As the West India trade increased from year to year the raising of horses became very profitable and many farmers entered into it largely. Lands being uninclosed it was easy to run such horses off to a port where the mark of the owner was not known, or the mark itself could be altered. A bold rover in the woods might entrap half a dozen horses with ease and, shooting them off through Indian paths by night, reach some port in a neighboring colony; and before the owner could get track of them they were far off upon the ocean, out of reach of proof. Many persons otherwise respectable entered into this practice or connived at it. Men who would scorn to pocket sixpence that belonged to another seemed to think it no crime to throw a noose over the head of a horse running loose and to nullify the signet of the owner or engraft on it the mark that designated their own property.

Professional buyers, called "horse coursers" in the parlance of the time, went about the country gathering up horses into pounds for sale or driving them to ports whence they were shipped, and very few of these persons escaped the suspicion of having at one time or another enlarged a drove by gathering into it some to which they had no legal claim. Persons of considerable prominence also were implicated, as Miss Caulkins indicates; William Coddington, at one time governor of Rhode Island, seems to have been one of these (96).

Such delinquency increased greatly in the latter half of the century and the disclosures become more and more frequent. In 1668, as a preventive measure, the Massachusetts Bay general court ordered a toll book to be kept in every town, in which was to be entered a description of each horse, and a voucher was to be given to the owner to prove his property (97). It was necessary to present this voucher in case of any subsequent sale. As has been noted, both Rhode Island and Connecticut had passed laws forbidding the taking of horses beyond their jurisdiction unless first recorded by the town recorder. In 1684 court was held at Stonington for the trial of horse coursers. Two persons were convicted and sentenced to pay fines of £10 and to receive fifteen lashes (98). The court calls the offense "a crying evil" against which all well-disposed persons were bound to give aid. In 1700 a special court was held at New London for the sole purpose of trying horse thieves, and the penalties for such thieving were made more severe (99). Finally, in 1701 a toll book was ordered to be kept in

every seaport town in Massachusetts, in which were to be entered the number, description, destination, and vessel on which it was shipped, of every horse sent out of the colony, as well as the name of the owner of the horse and his place of residence. For any violations a fine of £10 was to be inflicted for each horse sent out (100).

The incentive for most of this stealing was, of course, the export trade to the West Indies, which made the thieving both possible and profitable. The prevalence and widespread extent of this practice is but one more indication of the importance and magnitude of the export trade itself during this period. It is therefore probably no exaggeration to say that by the year 1700, horses were being raised for shipment to the West Indies throughout the whole New England area — to such an extent had the trade developed in the space of fifty years. It is apparent, however, that by this time a shift was taking place in the center of the trade, from its early location in the ports of Massachusetts Bay to those of Rhode Island and, especially, Connecticut.

These shipments of horses were carried on the decks of the vessels engaged in the West Indies trade, so that nearly every ship could transport a few animals on the southward voyage. Since the ships engaged in the trade were numerous and since they usually made two trips a year (101), the possible shipments of horses were large. By the end of the period, also, a beginning had been made in the building of vessels with more ample deck space to provide room for the livestock shipments, and these "horse jockeys," as such vessels were called (102), played an important part in the West Indies trade during the century that followed.

INCREASING DEMAND FOR NEW ENGLAND HORSES FROM 1700 TO 1775

The exportation of horses, which by 1700 had become a well-established part of the trade of New England with the British sugar colonies, continued on an increasing scale during the century that followed. About 1700, however, the demand for supplies for the islands began to be greatly augmented by the entrance into the market of the Dutch and French West Indies, which were beginning in their turn to develop the raising of sugar on an extensive scale. A steady increase in New England exports was a reflection of these changes that were taking

place in the sugar industry, and horses continued to be an important item in the exchanges. In the various ups and downs of the sugar trade, therefore, is to be found the explanation for corresponding changes in the raising of horses which took place in New England during the first half of the eighteenth century.

GROWTH OF THE SUGAR TRADE AND EXPANSION OF THE MARKET FOR HORSES.

In 1698 a decree of the Royal Council of France allowed sugar from the French islands, which were at that time producing only small quantities, to be sent directly to any port in Europe. This proved a great stimulus to the development of the French colonies, and after the Peace of Utrecht the growth of these was rapid (103). Martinique, Guadeloupe, Dominica, and Santo Domingo — the French colony on the island of Hispaniola, or Haiti — all came into the market with sugars. Prices fell off sharply as a result of the increased production (104), and the British islands — partly, at least, because of the law compelling them to send their sugar first to England, from whence it was re-exported[4] — found it difficult to compete with the French, who were soon in a fair way to oust the British from their leadership in the trade (105).

The continental British colonies were not slow in taking advantage of the new outlet for their products which was thus opened up, especially as the trade with the French proved to be very profitable. The French home market was closed to the importation of rum — which, distilled from molasses, was an important by-product of the manufacture of sugar — and as a result the French planters were willing to sell their molasses much more cheaply than were the British. This molasses was eagerly taken by the New England traders in exchange for the usual plantation supplies, and was brought back to New England, distilled into rum, and used to advantage in exchanging for furs and in the African slave trade.

Most of the trade with the French islands was carried on by direct voyages to their ports, and some supplies were furnished in this way

[4] According to Ashley (*The British Colonies in America*, vol. 1, app. 1, p. 75) the re-exports from England during the period under discussion were as follows: 1713–1715, 18,000 hogsheads a year; 1715–1719, 17,000 hogsheads a year; 1733–1736, 2300 hogsheads a year; 1737–1739, not more than 450 hogsheads a year.

to the Dutch, who were increasing their sugar production in Surinam. There grew up in addition a very considerable indirect trade by way of the barren Dutch island of Curaçao, where the Dutch had established a free port. This port soon became a great entrepôt for all the West Indies. Here were landed the supplies brought by the New England vessels, which returned home laden with sugar, molasses, and the other products of the islands, while the lumber, horses, provisions, and other supplies brought by them were either transferred directly to island vessels or put ashore and peddled out among the islands by the Dutch at their leisure (106).

During this time New England horses continued to be sent, as formerly, to the British islands along with the other customary supplies, but there is much evidence that they were equally important in the trade with the Dutch and the French. At Curaçao they were received in considerable quantities and many were put ashore on the neighboring islands of Boneiray (or Bonaire) and Aruba (107). Here they were kept until there was a call for them in the trade carried on at Curaçao. At Surinam no vessel was allowed to trade unless it brought in horses as part of its cargo (108), and the various reports to the Lords of Trade made by the governors of the continental British colonies indicate that this Dutch colony was a frequent destination for the horses sent out from their ports (109). Another and more confidential report made to the Lords of Trade in 1721 "On the State of the British Plantations in America" states that "the trade of Massachusetts Bay consists chiefly in the export of horses to Surinam and to Martinico and other French islands, which is a great discouragement to the planters in the British islands for without these horses French and Dutch could not carry on their sugar trade" (110). In 1743, Ashley, writing on the condition of the British colonies, also notes horses as one of the important items with which the French and the Dutch are supplied by the continental colonies (111), and his statement is confirmed by that of other contemporary writers and, especially, by reports of the various British governors to the Board of Trade in London.

There are many other indications that this trade in horses between New England and the Dutch and French islands was extensive. Gov-

ernor Robert Lowther, of Barbados, writing to the Board of Trade as early as 1715, states: "It would be of great advantage to this place, and to all his Majesty's Sugar Colonies, if there was made a law in England to Restrain His Subjects in North America from exporting Horses into any country not under his Majesty's Dominion, for the French at Martinique and Guadelupe and the Dutch at Soronam begin to rival us in the sugar trade and this is owing to the great Supplies of Horses they receive from New England" (112). Other British governors and numerous sugar planters continued to write to the Board of Trade in a similar vein, protesting especially against the trade between the northern colonies and the French, which they claimed was in violation of the treaty of neutrality made in 1686 between Great Britain and France.

The matter came to a climax in 1731, when the British planters presented a petition to Parliament with a draft of a bill which would specifically forbid the continental colonies to sell "horses, lumber, and provisions" to any but British subjects (113). Hearings were held on this bill and much evidence was brought out to indicate that the trade in horses was a very important part of this commerce. The testimony of a certain William Fraser is a fair sample of the large amount of evidence in this connection. In 1729 he claimed to have seen about thirty New England vessels at Martinique and St. Lucia trading horses for molasses, and he stated further that the New Englanders told him that if they brought in sixty horses alive they paid nothing for their permission to trade.

The continental colonies vigorously defended their right to trade with the French and the Dutch, and the bill finally failed to pass.[5] A long and acrimonious discussion ensued, finally resulting in the passage of the so-called "Molasses Act,"[6] which, by putting a prohibitive duty on the importation of foreign sugar, molasses, and sirups, aimed to put an end to the questioned trade. This act, however, because of the lack of adequate machinery for its enforcement, could not at that time be

[5] An incorrect statement to the effect that such sales of horses to foreign sugar islands were prohibited in 1731 appears in the volume on Rhode Island Commerce, Massachusetts Historical Society, Collections, 7th ser., vol. 9, no. 69, p. 14, note 2.

[6] 6th George II, Chapter 13. This act provided for a duty of sixpence a gallon on molasses and sirups, and five shillings a hundred pounds on sugar imported from any foreign American plantation into any British colony. Importations from Spanish and Portuguese sources were exempted, thus making the act in effect a hindrance only to trade with the French and the Dutch.

made effective — especially since it would have been fatal to a trade which had now become a vital necessity to the continental colonies. It was not until a considerably later time, when the restrictions were revived under Grenville's ministry, that the act really was enforced (114). The trade during the period in question therefore continued practically unchecked, and New England still succeeded in furnishing all the West Indies with horses as well as other supplies.

There is little doubt that during this time horses were a very important source of income to the New England colonies. They are invariably mentioned first among the products of Rhode Island in the reports made by the various governors to the Lords of Trade in London (115). The extent of the shipments is noted also by most of the contemporary writers of the period — "vast quantities of lumber and horses sent out by the New Englanders" (116), as one writer has described it. Some idea of the importance of the trade may be gained also from the complaints of the British planters, already mentioned, because of the supply furnished to their competitors, the French (117). The reports of the governors of New York during this period indicate that this colony also was exporting some horses at this time (118), but not in sufficient quantities to threaten the leadership of New England in the trade.

CONTRABAND TRADE DURING THE FRENCH AND INDIAN WAR

During the years from 1755 to 1763, the period of the struggle between France and Great Britain for supremacy in America, the trade of all the islands of the West Indies suffered more or less. The French sugar planters especially, because of British dominance on the sea, were often in serious difficulties. Nevertheless, plantation supplies continued to be sent out from the continental colonies to both British and French islands. The trade with the French islands was of course contraband, but through various devices it continued to be conducted on a very considerable scale, and by this means French sugar and molasses still found an outlet and the needed supplies were obtained.

Some of this trade with the enemy on the part of the continental colonies was carried on directly under the protection of flags of truce granted by the colonial governors for the ostensible purpose of exchang-

ing prisoners, and in other ways. A very considerable part of the contraband trading, however, was of a more roundabout sort and was effected through the neutral Dutch and Spanish ports. At first the Dutch islands of Curaçao and St. Eustatius were the centers of this trade, but, being broken up in these places by the British fleet, the trade transferred itself to the Spanish port of Monte Christi adjacent to the French settlements on the island of Haiti. Here resorted New England vessels laden with the customary plantation supplies, which they exchanged at very profitable rates for French sugar and molasses in addition to bringing in European goods and taking back part payments in coin (119).

Thus, in spite of difficulties, it was still possible to find an outlet for New England horses, and these continued to be supplied to both French and British planters. This is indicated, for example, by the complaint of Governor Hardy to the Lords of Trade in 1757 to the effect that the New England colonies still continued to send supplies to the enemy. Governor Hardy mentions a privateer "lately come into port which reports having spoke several vessels off Block Island bound for the Indies with horses notwithstanding the general embargo agreed on by the several governors" (120). In 1762 also the British fleet in the Bahamas seized a similar vessel bound for Cayenne with lumber, provisions, and horses (121).

After the conclusion of peace between France and Great Britain in 1763, the commerce between the northern colonies and the British islands went on as before. Between that date and the beginning of the American Revolution, horses were again a considerable item of exchange. In the years 1771 and 1774, according to the record of the Secretary of Customs in London, there were imported into the British islands from "North America" a total of 3647 oxen and 7130 horses (122). The trade with the French islands, however, fell off considerably because of the resurrection of the Molasses Act and the establishment of means for its adequate enforcement, as well as other trade acts that were passed (123).

CHANGES IN THE PRODUCTION OF SUGAR

In addition to the effect of the continued growth of both British and French sugar plantations throughout this period, with the various inter-

ruptions in the trade resulting from wars, acts of Parliament, and other causes, there remained still another factor that affected the demand for horses. This was a change in the methods of manufacture of sugar, which took place in connection with a shift in the center of production from the small islands, such as Barbados, Antigua, and Guadeloupe, to the larger ones such as Jamaica and Haiti.

The advantages of the larger islands for the production of sugar were numerous, and they early became apparent to both the British and the French. In both Jamaica and Santo Domingo there were extensive savannas where pasturage was abundant, and the planters thus were able to produce in some measure the livestock needed for draft purposes on the plantations as well as some to be used for food; in addition, both islands were well stocked with wild horses and cattle left from the former Spanish occupation; (124) and, further, there was plenty of timber to be found, of a sort which could be used in constructing sugar mills.[7] In Jamaica, at least, sugar could be cured more quickly than in the islands of the Windward group (125). Another factor, probably of more importance than any of the others, was the presence of numerous streams capable of furnishing water power for turning the heavy cylinders of the cane-crushing mills (126). All of these conditions tended to facilitate the production of sugar, and as a result Jamaica and Santo Domingo were enabled to increase their output at a more rapid rate than the small islands could do.

The use of water power for driving the cane mills naturally removed the need for horses and cattle for this task. A similar displacement took place to some extent even in the colonies not possessed of adequate water power. In such colonies resort was had to wind-driven mills, and in Barbados, for example, according to Oldmixon, there were by 1741 forty mills of this type to one of the earlier sort (127). On the whole, however, there probably remained in operation a very considerable number of the older horse and cattle mills, and this, together with the fact that they were still needed to haul supplies and to bring the canes from the field, continued to make horses an important item in the

[7] Jamaica was taken by the English from Spain in 1655, and was found to be so well stocked with horses and cattle that it was at once proposed to supply Barbados and the other British colonies from there. This plan was given up, however, because of the difficulty of sailing from Jamaica to the Windward Islands due to the prevailing winds.

needed supplies for the sugar plantations. Also, in Jamaica and in Santo Domingo, in spite of their own abundance of livestock, numerous instances are recorded of their continued importation throughout the period (128). Lastly, the demand for saddle horses was a continuous and important one in all the sugar colonies and, further, was a demand which grew with the general increase in the wealth of the planters. In short, it would seem that whatever decrease in the demand for horses may have resulted from the shift in the center of sugar production and changes in the method of manufacture, such decrease was fully balanced by the mere aggregate of the demand from the steadily increasing number of the plantations and the extensiveness of their operations.

Throughout the whole period from 1700 to 1775, therefore, there existed in the West Indies a ready market for horses which was taken full advantage of by the New England colonies, following the beginning already made in this sort of trade before 1700. During the later period, however, the trade was not confined to the British islands, as formerly, but had extended to those belonging to the Dutch and the French as well; it was better organized and on a much more extensive scale; and, though interrupted in various ways from time to time, it had come to be an important part of the commerce of New England and remained so until the War of the Revolution.

DEVELOPMENT OF COMMERCIAL HORSE RAISING FROM 1700 TO 1775

The steadily widening market for horses which was opened up during the period from 1700 to 1775 has just been described. It is apparent also, from the evidence given, that New England took full advantage of the opportunity for exporting horses which was thus presented. There now remains to be considered the resulting development which took place in New England itself during this same period, whereby the raising of horses on a commercial scale became an important industry.

For the beginning of this development no exact date can be set, but early efforts along this line before 1700 have already been indicated — as, for example, the plans of John Hull and his associates in the Pettiquamscut Purchase in Rhode Island. Most of the early shipments of horses to Barbados and the other British colonies prior to 1700, how-

ever, were in the nature of a disposal of an already existing surplus of horses. But with the settlement of Rhode Island and Connecticut these regions soon adopted the raising of horses for export as a regular source of income, and their ports at length came to displace those on Massachusetts Bay as leaders in the trade.

Some of the reasons for the development of the industry in the newer regions have already been indicated. The broader and more level lowlands, extensive salt marshes to furnish hay, lagoons and ponds to serve as natural boundaries for the pastures, all combined to give these regions an advantage. To this should be added the fact that much of this abundant marsh and other forage was easily accessible for boats, which could make their way into the numberless small streams and inlets and there be loaded with little difficulty.[8] This was a matter of no small gain when it is remembered how difficult it would have been to transport such a bulky commodity as hay over the rough frontier roads of the period. Forage of some sort was a very necessary part of the cargo of the vessels carrying horses to the Indies, for the horses must be fed in transit, and the hay, even though it was commonly pressed into rough bales (129), was an unwieldly article to handle; while the horses themselves, if necessary, could be driven long distances to the point of embarkation.

The development of horse raising as an industry in Rhode Island and Connecticut went hand in hand with the development of the commerce of these colonies with the sugar islands. Its extent, however, must mainly be inferred from mention of it in the reports of the various governors to the Lords of Trade in London and from such fragmentary records of actual shipments as are available.

EXPORTATIONS FROM RHODE ISLAND PORTS

The Rhode Island ports were the first in the new region to embark in the export trade, and even as early as 1681 horses are mentioned by Governor Sanford as one of the " principall matters of export " (130). In the next twenty years the shipping had increased " sixfold " and horses were being sent to Jamaica, Barbados, Nevis, Antigua, St.

[8] As early as 1749, hay was being shipped from the region by boat to other places in New England which were less well supplied. (Elliot, *Essays upon Field Husbandry*, 2d, p. 21.)

Christopher, Montserrat, and Surinam (131). In 1731 Governor Jenks places them first in importance among the exports of the colony, and states that at that time there were ten or twelve vessels engaged in the West Indies trade (132). Ten years later the number of vessels had grown to one hundred and twenty (133). Douglass also confirms the importance to the Rhode Islanders of horses as an article of commerce (134), while the Reverend James MacSparran, for a long time resident in the colony, tells of the "fine horses which are exported to all parts of English America" (135).

Newport and Providence were the main ports of embarkation, but many horses were shipped on small vessels directly from the farms in the Narragansett country (136), where was found the greatest center of the livestock production. In 1745 Moses Brown, one of the more prominent of the Providence merchants, had eight vessels under his management, "some to Surinam with horses" (137); while the correspondence of one Newport firm indicates that during the years from 1731 to 1773 this firm was shipping horses as a regular part of its cargoes to all the British islands and to Curaçao (138).

EXPORTATIONS FROM CONNECTICUT PORTS

At the outset the horses sent out from Rhode Island came into competition with those that continued to be sent from the Massachusetts Bay region, but before long it was Connecticut that had come to be the chief rival in the trade.[9] The renewed enforcement of the Molasses Act after the close of the war with France in 1763 dealt a hard blow to the commerce of Rhode Island, which had been the chief center for the distillation of rum from the molasses received from the French islands,[10] and with the considerable decline in its trade which followed went a lessening of the exportation of horses from its ports and a partial diversion of the trade to the easily accessible outlet at New London in Connecticut, where such shipments had for some time been well established.

[9] One Newport captain in 1731 quaintly complains to his owners that he has been unable to dispose of his cargo of horses at Antigua because "there was 3 New London men arrived before I landed. They sold there horses for tow pistoles a head which is true." (Massachusetts Historical Society, Collections, 7th ser., vol. 9, no. 69, p. 16.)

[10] The former prohibitive duty of sixpence a gallon was reduced in 1764 to threepence; and the act was finally repealed in 1766 and a tax of only one penny a gallon was imposed instead. But between the war and these duties, Rhode Island commerce suffered heavily.

In addition to those shipped from New London, many Connecticut horses were put directly aboard ship at the towns on the Connecticut river, especially at Windsor, which had a considerable trade with the West Indies (139); and after the middle of the century, considerable numbers were sent out from New Haven. New London, however, was the chief point of embarkation, and many horses, as well as other livestock, were driven in from other colonies to be sent from there to the southern market (140). All the Connecticut vessels were supposed to clear at this port (141), and some of the river vessels undoubtedly took on board their cargoes of horses there (142), although, according to Caulkins, many such vessels "slipped over the bar uncounted" and sailed directly to the Indies (143).

This commerce of the Connecticut coast towns was well known. James Fenimore Cooper, in one of his tales of frontier life written at a date (1832) near enough to the heyday of this trade to have enabled him to get direct testimony as to its extent, puts the following in the mouth of one of his characters: "I have been down at the mouth of both Havens, that . . . named after the capital of Old England, and that which is called Haven with the addition of the word 'New,' and have seen the snows and brigantines collecting their droves like the ark, being outward bound . . . for barter and traffic in four footed animals" (144).

The Connecticut vessels were mainly sloops and schooners, single-decked and without topmasts; and, unlike those of the other colonies, they were engaged almost entirely in the West Indies trade, making two trips a year. In New London, however, there were built some larger square-rigged ships, with more ample deck space designed to facilitate the transportation of large cargoes of livestock. These "horse jockeys," as they were called, have already been mentioned; one of them sailed from New London in 1716 bound for Barbados with forty-five horses on board, and later others were built which could carry even greater numbers (145). In 1724 six of these ships left port together, all freighted with similar cargoes (146), and in 1731 three arrived in Antigua with so many horses as to completely swamp the market (147).

Taken as a whole, the commerce of Connecticut increased very rapidly during this period and continued to increase until the beginning of

the Revolutionary War,[11] and from all the evidence available it is clear that the export trade in horses played no inconsiderable part in this growth. Horses continued to be sent out from Rhode Island and Massachusetts ports, but it was in Connecticut, and especially in New London, that the trade finally came to be mainly centered in the period just before the Revolution.

SOURCES OF SUPPLY FOR THE EXPORT TRADE

Such an extensive exportation of horses from the Connecticut and Rhode Island ports as has just been described indicates the raising of them for this purpose in large numbers and over a very considerable area. Details concerning such horse breeding, however, are very meager. Horses were probably raised to some extent by all the farmers in the region in response to the steady demand that existed.[12] The various cases of horse stealing found in the court records, as already described, as well as the presence of the so-called "horse coursers" who went about the country buying up animals and driving them in herds to the points of shipment, would indicate that this was the case (148).

Here and there throughout the area, however, were certain favorably situated districts where the breeding of horses and of other animals for export was much more specialized. This was the case, for example, on Fisher's Island, just off the mouth of the Thames, which was given over almost entirely to animal husbandry (149). Also, in the Connecticut River Valley the region round about Windsor seems to have been another such center (150). But by far the most extensive and important of these specialized areas was to be found in the Narragansett district of Rhode Island — a region so famed in the annals of the time for its great flocks of sheep, its dairies and cattle, and above all its fine horses, as to have been noted by most of the contemporary writers of the period.

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[11] Between the years 1762 and 1774 the number of Connecticut vessels increased from seventy-six, with a total burden of 6790 tons, to one hundred and eighty, with a total tonnage of 10,317. (Connecticut Archives, Census, p. 5. Cited by Weeden, *Economic and Social History of New England*, vol. 2, p. 758.)

[12] The inventory of John Walworth, of New London, in 1748 shows the arrangement of a well-to-do farmer's estate of that period. He possessed 4 negro servants, 77 ounces of silver plate, 50 head of cattle, 812 sheep, and 32 horses, mares, and colts (Caulkins, *History of New London*, p. 345).

THE NARRAGANSETT PLANTERS AND THEIR HORSES

Strictly speaking, the Narragansett country embraced all the lands occupied by the Narraganset Indians at the coming of the English; but in the parlance of the time the term came to be applied to a part of this territory consisting of a strip of land about twenty miles long and from two to four miles wide. This extended along the western shore of Narragansett Bay, from Wickford on the north to Point Judith on the south, and thence westward along the coast to include the Champlain tract in Charlestown. It was on this fertile, well-watered plain that there was developed a region of large and pretentious estates — the homes of the Narragansett planters, so called — and here was found a type of agriculture and a social order unlike anything to be found elsewhere in New England.

Channing, who has had access to the local town records of the area and to various manuscripts and family papers, describes these Narragansett planters as follows (151):

> Unlike the other New England aristocrats of their time these people derived their wealth from the soil and not from success in mercantile adventures. They formed a landed aristocracy which had all the peculiarities of a landed aristocracy to as great an extent as did that of the southern colonies. Nevertheless these Narragansett magnates were not planters in the usual and commonly accepted meaning of the word. It is true enough that they lived on large isolated farms surrounded by all the pomp and apparent prosperity that a horde of slaves could supply. But if one looks beneath the surface, he will find that the routine of their daily lives was entirely unlike that of the Virginia planters. The Narragansett's wealth was derived not so much from the cultivation of any great staple like cotton or tobacco, as from the product of their dairies, their flocks of sheep, and their droves of splendid horses, the once famous Narragansett pacers. In fine they were large — large for the place and epoch — stock farmers and dairymen.

This region was from the outset one of large-scale agricultural operations. Roger Williams had penetrated the area some time before 1650, and in 1641 Richard Smith had bought a tract of 30,000 acres from the Narraganset sachems and had erected a house (152); but the real settlement of the area did not proceed at a rapid rate until after the Pettiquamscut Purchase (153), made in 1657 by John Hull (of pine-tree shilling fame) and a number of associates, and the Atherton Purchase (154), made two years later by a company headed by Sir Humphrey Atherton and John Winthrop, of Connecticut. Both these groups of owners bent their efforts to obtaining settlers for their holdings. Evidently, because of the many natural advantages of the sec-

tion, they had little difficulty in achieving this result, for in 1670 a letter from Major Mason to the Commissioners of the Colony of Connecticut stated that the land was at that time mainly taken up with farms, some of which were five, six, and even ten miles square (155). John Hull's plan in 1677 for horse breeding on a large scale to get "large and fair horses and mares" for the West Indies trade is noted elsewhere and is another evidence of these large-scale operations. Hull's scheme was a rather ambitious one. He planned to build a stone wall across Point Judith Neck, which would have inclosed a peninsula approximately five miles long and having an average width of about a mile. The object of the wall was to keep out mongrels and strays so that the planters would thus be able to breed up a stock of horses of superior characteristics for shipment to the Indies. Hull goes even further and suggests to his partners, "We might have a vessel made for that service, accommodated on purpose to carry off horses to advantage" (156).

The wealth of the district increased steadily up to the time of the Revolution, and full use was made of the opportunities for animal husbandry of an extensive sort. In 1755 Douglass notes that for New England, "the most considerable farms are in the Narragansett country," and that the largest of these "milks 110 cows, cuts about 200 load of hay, makes about 13,000 weight of cheese besides butter, and sells off considerably of calves, fatted bullocks, and horses" (157). In 1747 South Kingston, the center of the Narragansett region, was assessed for the public colony rate a sum only a little less than that for Providence and about half that for Newport (158); in 1780 it had become by far the richest town in Rhode Island, paying double the sum assigned to Newport and two-thirds more than Providence (159). Most of this wealth was apparently derived from agricultural operations.

Their cattle and the output of their dairies were an important source of revenue to the Narragansett planters. But by far the most noted product of the region — at least toward the middle of the eighteenth century — was a breed of saddle horses which they developed.[13] These

[13] The preference for pacers appeared at an early date and obviously is the cause of the development of the Narragansetts themselves through selection and breeding. Thus Waite Winthrop writes from Boston in 1684 concerning some horses consigned to him for sale: "I am offered £30 but if the two paced well they would bring nearer £50, for such is difference from ordinary jades if they do but pace well." (Winthrop Papers; Massachusetts Historical Society, Collections, 5th ser., vol. 3, p. 446.)

were the famous Narragansett pacers, whose praises were sung by all the contemporary writers of the period and tales of whose remarkable performances still linger as part of our American horse lore.

The best description of these unusual pacing horses is given in an article on American agriculture in the first American edition of the Edinburgh Encyclopedia (160), written about 1830 by Robert Livingston. The description reads as follows:

> They have handsome foreheads, the head clean, the neck long, the arms and legs thin and taper; the hindquarters are narrow and the hocks a little crooked, which is here called sickle hocked, which turns the hind feet out a little: their color is generally, though not always, bright sorrel; they are very spirited and carry both head and tail high. But what is most remarkable is that they amble with more speed than most horses trot, so that it is difficult to put some of them upon a gallop. Notwithstanding this facility of ambling, where the ground requires it, as when the roads are rough and stony, they have a fine easy single footed trot. These circumstances, together with their being very sure footed, render them the finest saddle horses in the world; they neither fatigue themselves nor their rider. It is generally to be lamented that this invaluable breed of horses is now almost lost by being mixed with those imported from England and from other parts of the United States.

The sturdy qualities of the Narragansett pacers have been perpetuated also by James Fenimore Cooper in his tales of the American wilderness. The horses were evidently still obtainable in Cooper's day (161) and he must have been an admirer of the breed, for he brings them into his stories frequently. They are described by Cooper as being small, sorrel in color, and distinguished by their easy pacing gait and great endurance.

As to the origin of these pacers — the first distinctly American breed of horses — there have been many stories current at one time or another, most of which tales are obviously fanciful. One of the most plausible accounts is a tradition handed down in the Hazard family, of Rhode Island, the early members of which were among the more important breeders of the animals. According to this story the progenitor of the breed was imported from Andalusia, in Spain, by Deputy Governor Robinson (162), whose estate the Hazards inherited.

Wallace (163), a modern writer who has given some attention to the various stories regarding the origin of the Narragansetts, contends that they resulted solely from careful selection and breeding of the common New England stock. He refuses to give credence to the story

of an admixture of Spanish blood, first, " because there were no pacers in Andalusia or any other part of Spain," and secondly, because " the Narragansetts were a leading article of export from Rhode Island in 1680, thirteen years before Governor Robinson was born." Both these objections made by Wallace are of doubtful validity, however. There is available no such complete information regarding the horses in Spain during the period in question as to justify any such sweeping assertion as to the entire absence of pacers. And, although it is true that horses were reported by Governor Sanford to the Lords of Trade in London in 1680 as an important article of export from Rhode Island, there is nothing to indicate that these horses were of the Narragansett breed. The presumption is that they were not, for the Narragansett district proper was not really settled until about that date. Furthermore, Captain John Hull in 1677 looked on his plan (noted on page 905 for breeding a race of " large and fair horses and mares " as a new venture for the region. In short, the horses mentioned by Governor Sanford were in all probability raised in the northern and eastern parts of Rhode Island, where the country was already in farms before the Narragansett district was settled.

It would seem, therefore, that the tradition concerning the importation of Spanish stock by Deputy Governor Robinson deserves some credence. Whether or not there were any pacers in Spain at the time is immaterial, for it is shown by the correspondence of Governor Winthrop and other writers that pacers were not uncommon in New England as early, at least, as 1684 (164), and the pacing gait of the Narragansetts may very easily be accounted for on the basis of selection and breeding of this native stock. Such selection may have gone on for a greater or less period before the importation of a stallion from Spain to still further improve the breed. Such importation, in fact, is just what might have been expected to happen as attention was increasingly directed to developing an improved strain.

The pacing gait was one of the most characteristic points of the Narragansetts. It is said that the pure-bloods could not trot at all. The gait itself is described as being peculiar in that the backbone of the horse moved through the air in a straight line, thus differing from

that of the common "racker," or pacer of the present day, and from horses having an acquired pacing gait (165). A breed in which the pacing habit was so firmly established must have had back of it an ancestry in which such movement had long been the usual gait. As already indicated (page 894), such a breed is to be found in the Irish hobbies, which were so greatly sought after as saddle horses in England during the early part of the seventeenth century mainly because their pacing gait was easier than that of any other horses of the period. Such fragmentary descriptions of these hobbies as are available (166) disclose a striking similarity in appearance to the Narragansett pacers. These Irish ponies were small, spirited, possessed of unusual endurance, and commonly sorrel in color — all of which characteristics are similarly to be found in the Narragansetts. Although no direct proof can be adduced in support of such a view, it would seem to be at least a plausible theory that the Narragansett pacers resulted from the selection and breeding of some of these Irish hobbies which had been brought to New England at an early date. Later, as indicated by the tradition in the Hazard family, these may have been crossed with some imported Spanish stock to build up the breed still further.

As to the speed and stamina of the Narragansetts and the unusual ease of their gait for saddle purposes, there is much evidence. Pacing races were often held at Little-Neck Beach at South Kingston, and some of the silver tankards won at these races are said by Updike, writing in 1847, to have been still in the possession of some of the old Narragansett families at that time (167). The Reverend James MacSparran, sent out to Rhode Island in 1721 by the Society for the Propagation of the Gospel in Foreign Parts and for many years a resident in the colony, records that he has seen some of these horses pace a mile "in a little more than two minutes and a good deal less than three," and adds further that he has often ridden them "fifty; nay, sixty miles in a day even here in New England where roads are rough, stony and uneven" (168). Another contemporary writer describes "the natural pacers of horses which at a cow run — a gait which they acquire by pasturing when colts with the cows [truly a surprising theory!] — will pace three miles in seven minutes."

Further evidence of the unusual ease of the saddle gait of the

Narragansetts is given in a letter written about 1847 and quoted by Updike (169) in his *History of the Episcopal Church in Narragansett.* This describes how in 1791 an aged lady then living in Narragansett rode one of these pacers on a lady's side-saddle to Plainfield, a distance of thirty miles, rode the next day to Hartford, forty miles, staid in Hartford for two days, then rode forty miles to New Haven, then forty miles to New London, and then home to Narragansett, forty miles more. The lady claimed to have experienced no sensible fatigue.

Because of the export trade with the West Indies, horses of any sort would have been a valuable source of revenue to the Narragansett planters,[14] and it is probable that many of the ordinary New England stock were bred for this purpose in the region. But the cream of the demand from the sugar planters was for saddle horses for personal use, and for these they were willing and able to pay extravagant prices. To this demand was added that of persons of means throughout all New England and the other continental British colonies as well.[15] Thus, in these unusual pacers, whose gait and general characteristics suited them so admirably to such use, it is clear that the Narragansett district had a very important source of revenue and one which probably contributed in no small measure to its prosperity.

The horses and other livestock of the Narragansett district designed for exportation to the West Indies found an outlet through the various ports on Narragansett Bay, or were driven to New London or Stonington over the old Pequot trail, which had become the post road between Boston and New York and which passed through the center of the region. Apparently many animals were shipped also directly from the Narragansett country itself; Robert Hazard, for example, is said to

[14] From the account book kept by Thomas Hazard, one of the wealthiest and most prominent of the Narragansett planters, may be gleaned some idea of the prices received. In 1753 he sold a three-year-old at £150, and the next year a thirteen-year-old bay "with a white nose" brought £70; while in 1755 a "black troting mare" brought only £55. In 1763 a black mare sold for £244, but by that time the Rhode Island currency had greatly depreciated in value and Mr. Hazard noted alongside that £7=1 Spanish Milled Dollar." In 1766, however, one "dark colored natural pacing horse with some white on his face" brought the high price of fifty-five Spanish milled dollars. (Hazard, *Thomas Hazard, Son of Robt., call'd College Tom.* p. 63.)

[15] Watson (*Annals of Philadelphia and Pennsylvania,* p. 209) gives an account of one such shipment in 1711, as recorded in a letter written by a certain Rip van Dam who had engineered the transaction on behalf of Jonathan Dickinson, of Philadelphia. The horse was shipped from Rhode Island in a sloop, from which he jumped overboard and swam ashore to his former home. Recaptured, he finally arrived in New York, "after fourteen days passage much reduced in flesh and spirit." He cost £30 plus 50 shillings for freight, and was evidently an animal of spirit; he "would not stand still but plays about all the time;" he would "drink a glass of wine or beer or cider," and Rip van Dam further opines that "he would drink a dram on a good cold morning."

have raised about two hundred horses annually and to have loaded two vessels a year with them and other produce of his farm. These vessels sailed " from the South Ferry directly to the Indies where the horses were in great demand " (170). It was the Hazard family [16] which seemed to have been mainly concerned in the early development of the Narragensett pacers, and it is probable that many of the horses thus shipped were of the famous breed.

To recapitulate, then, it may be said that during this period from 1700 to 1775, in response to the demand from the West Indies sugar plantations for draft animals and from the same source and from all the continental colonies for saddle purposes, the breeding of horses finally became, in the period just preceding the Revolution, a widespread industry throughout all Rhode Island and Connecticut — and probably in the other New England colonies as well — and that in some particularly favored spots it was carried on in a highly specialized and extensive fashion. The " horse jockeys " with their large cargoes, the numberless small vessels carrying only a few animals on their scanty decks, the famous pacers driven overland to neighboring continental colonies, all must have contributed a very considerable item of revenue to the New England region and aided the colonists in that search for " a good return " on which they were always bent.

DECLINE IN HORSE RAISING AFTER THE REVOLUTION

The exportation of horses, which was interrupted during the Revolution as was the other commerce of the colonies, was revived at the close of the war. Now, however, the New England vessels were denied entrance to the British sugar islands by the decree restricting trade to British bottoms, so that a considerable proportion of the former outlet for horses no longer existed. Such shipments as were made went mainly to the French islands and to Cuba, which by that time had been thrown open to trade by the Spaniards and was developing rapidly as a producer of sugar.

This revival of the horse trade seems to have had its main focus in New London. The " horse jockeys " were once more embarked on their former service; one brig took out forty-nine horses, and many sloops

[16] The Robert Hazard mentioned above was born in 1689 and died in 1762.

carried as many as thirty-five in a single cargo. The *Enterprise,* bound for Demerara, carried provisions, brick, lumber, twenty horses, seventeen neat cattle, and seventeen mules, besides swine, geese, and turkeys (171). The general extent of these shipments is shown in a marine list kept by Thomas Alden in the *New London Gazette.* According to this record there was sent out from New London during the year 1785 a total of 8094 horses and cattle; and in the years following, the numbers were, successively, 6671, 6366, and 6678 — the record ceasing with the year 1788 (172).

This revival of horse exporting apparently was not especially successful and did not continue long,[17] for the New London vessel owners were soon casting about for some better occupation for their ships. On the return of two of these ships from an expedition to the Gulf of St. Lawrence with profitable cargoes of whale oil, the *New London Gazette* exhorts, in rather mixed metaphor, "'Now my horse jockeys, beat your horses and cattle into spears, lances, harpoons and whaling gear, and let us strike out" (173).

The reopening of the British West Indies ports to New England vessels in 1789 (174) apparently failed to halt the decline that had begun in the New England horse trade, if one is to judge by the infrequency with which this trade is now mentioned. It is probable that in the general interruption of the trade during the Revolution, the sugar islands, thrown on their own resources, had learned to furnish their own supply (175). As already indicated, the larger islands of Jamaica and Haiti were plentifully supplied with pasturage and wild horses, by means of which this could be accomplished. Nor was Cuba as promising a market as might have been expected, for it possessed similar advantages. In addition, the substitution of water power for the mills probably continued to take place in all the islands where it was possible. Lastly, there are indications that the pasturage available in New England itself was not so ample as formerly and was being

[17] An indication of the general decline in the exportation of horses which occurred after the Revolution is found in the following table reproduced from Pitkin (*A Statistical View of the Commerce of the United States of America,* p. 62–63). These figures include shipments from other ports besides those in New England.

Year	1791	1792	1793	1794	1795	1796	1797	1798
Number of horses exported from the United States	6,975	5,656	3,728	3,495	2,626	4,883	1,177	2,132

gradually infringed on by the cultivation of new land; in fact, according to Elliot (176) this scarcity of pasture land and meadows, with the resultant high price of hay, had begun to be felt even before the Revolution. All these things combined to make difficult the resumption of the trade in horses on its former scale.

Just what became of the large number of animals which had for so long furnished a steady article of commerce is not very clear. The very considerable shipments to the French islands, already noted, which immediately followed the close of the Revolution, probably accounted for such surplus of the ordinary stock as had accumulated; while the demand for saddle horses on the part of the increasingly prosperous Spanish planters of Cuba probably took many of the Narragansett pacers (177). Then, too, the mere cessation of breeding new colts, as the demand for export purposes lessened, would have had an immediate effect on the numbers. But most important of all, doubtless, was the breaking up of former pastures for the purpose of cultivating field crops to supply the demand of Europe for provisions during the war between France and England which began in 1793 and which soon forced prices for such supplies to a high level. The effect of such a change in agriculture would be, on the one hand, to cut down the number of horses that could be cheaply raised, and, on the other, to give ample opportunity for the employment in the new operations of the horses already available. Finally, as the people from New England pushed westward to the settlement of newer lands in New York and elsewhere, they also probably drew off considerable numbers from the existing supply.

Another event indicating the changed conditions in horse raising as a New England industry during this period following the Revolution, was the disappearance of the Narragansett pacers. This breed, so carefully developed and so noted in the annals of the time, at length became extinct and is known at present only as a sort of legendary strain whose connection with other American breeds, if any connection exists, is mainly a matter of conjecture.

The demand for the Narragansetts from the wealthy planters of Cuba, when that island at length began to cultivate sugar extensively, has been assigned by one writer (I. P. Hazard) as the chief cause for the disappearance of the breed. He says in part: "The planters became suddenly rich and wanted pacing horses . . . to ride, faster than

we could supply them, and sent an agent to this country to purchase them on such terms as he could . . . He commenced buying and shipping till all the good ones were sent off" (178).

It is easy to understand that such a large and unexpected demand from Cuba, without restriction as to price, might deplete the breed very seriously. But if the Narragansett planters did thus actually kill the goose that laid the golden eggs by shipping off all their breeding stock, it must be that there were other factors at work which made them willing to sell. It might indicate, for example, that their experience in attempting to sell in their former markets after the war, had convinced them that the end of the earlier export trade was in sight.

There are, however, other obvious reasons which probably contributed to the dispersal of the sturdy little pacers which had so long been a profitable commodity. They were not beautiful at best; they were small, scarcely more than fourteen hands high, and their gait, while desirable for saddle purposes, did not fit them for driving to advantage in team or harness (179). All these things undoubtedly worked against the Narragansetts as the roads in the colonies became better, wheeled vehicles came into use, and there was need for larger and heavier animals for harness and draft. The pacers were, in short, of most value under frontier conditions, and as the region along the coast became more settled there is evidence that they were actually dispersed to remoter regions, especially to Canada, Kentucky, and Tennessee. It is in these places that the pacing blood seems to have been preserved in the midst of the influx of English thoroughbred stock beginning about 1750 (180).

Thus closed the final chapter in New England's leadership in the exportation of at least one product of an agricultural nature — a leadership which had been held undisputed for more than a century; which in the lean years of her early commerce had eked out to good purpose the exchanges of New England with the West Indies and by which she was enabled in turn to purchase English goods; which had aided in the opening and settlement of her lands remote from the coasts and harbors; and which finally had a part in the development in the Narragansett district of a social and economic organization based on agriculture, which was comparable to any other found in continental America during the colonial period.

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INSECTS AND OTHER ANIMAL PESTS INJURIOUS TO FIELD BEANS IN NEW YORK

I. M. HAWLEY

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CONTENTS

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I. M. Hawley

In June, 1917, a laboratory was established at Perry, in the bean-growing section of western New York, for an investigation of the diseases and the insects that had been causing much injury to field beans. In this work the Departments of Entomology, Plant Breeding, and Plant Pathology at Cornell University were each represented by one member. This investigation has been carried on for four years, and the results, on the whole, have been satisfactory. The entomological work, however, has been hindered by one unavoidable circumstance: in some summers the insect pests under investigation were very scarce, and field experiments for their control were thus impossible. As a result, the recommendations in some cases are based on fewer data than the writer had wished.

The more important part of this investigation is the part concerning the seed-corn maggot (*Hylemyia cilicrura* Rond.). The field gray slug (*Agriolimax agrestis* L.), a mollusk of the family Limacidae, also has been studied in detail, and some attention has been given to the green clover worm (*Plathypena scabra* Fab.), the red-headed flea beetle (*Systena frontalis* Fab.), the pale-striped flea beetle (*Systena taeniata* Say), the blue-banded millepede, or thousand-legged worm (*Julus caeruleocinctus* Wood), and the bean weevil (*Acanthoscelides obtectus* Say). Observations were made also on the habits of some insects of lesser importance, in particular those that produce the pitting of the bean known as *dimpling*.

THE SEED-CORN MAGGOT
(*Hylemyia cilicrura* Rond.)

It is difficult to obtain exact data concerning *Hylemyia cilicrura*,[1] for it is an erratic insect that may occur in a field in great numbers in one season, and not reappear in, or even near, that field the following year. The flies usually disappear in late summer and the hosts of the larvae during that part of the year are not definitely known. Reared flies apparently do not mate in captivity. Infestations of the insect in cultivated crops are not usually found until considerable damage has been caused. By that time the maggots are full-grown and it is too late for control experiments with that brood. The writer realizes the many gaps in the present work, but, as the insect is scarce at the present time, it seems desirable to record the results thus far obtained.

[1] This species is more commonly known in American literature on economic entomology as *Phorbia fusciceps* Zett.

SYSTEMATIC POSITION

The parent insect of the seed-corn maggot (*Hylemyia cilicrura*, Plate LXIX, 1) is a fly of the order Diptera and the family Anthomyiidae. The insect was first described by Rondani (1866)[2] as *Chortophila cilicrura*. Until recently, however, *cilicrura* has been considered synonymous with *fusciceps* of Zetterstedt (1845), and, since Zetterstedt's description precedes that of Rondani, *fusciceps* has been accepted as the specific name of the insect. Stein (1916) finds that *fusciceps* is a distinct species and not the *cilicrura* of Rondani. Malloch (1920) accepts the separation of the two species made by Stein. The species *fusciceps* of Zetterstedt occurs in Lapland and other parts of northern Europe, and recently Malloch (1920) has recorded it from North America. The species *cilicrura*, in addition to a wide European distribution, is present in most parts of North America, and is the pest known as the seed-corn maggot. The *fusciceps* described by Slingerland (1894) is not the *fusciceps* of Zetterstedt but is *cilicrura* Rond.

Stein (1916) places *cilicrura* in the genus Chortophila, but Malloch (1920) unites the genera Chortophila, Phorbia, and Hylemyia in the strict sense, in the genus Hylemyia. If we follow this latest paper on the subject, the seed-corn maggot must be called *Hylemyia cilicrura* Rond.

In the recent European writings of Reh (1913) and Oberstein (1916), the specific name *Chortophila cilicrura* is applied to this insect; but in older works, such as that of Ritzema Bos (1890), mention is often made of *Anthomyia platura*. The species *platura* is a composite of *cilicrura* and *trichodactyla*, and often it is impossible to determine definitely which species was blamable for the work these authors have described.

COMMON NAMES

The common names given to *Hylemyia cilicrura* include the following: deceiving wheat fly, locust-egg anthomyian, Anthomyia egg parasite, seed-corn maggot, corn Anthomyia, seed-corn flower-fly, bean maggot, bean fly, fringed anthomyian. Of these, the name *seed-corn maggot* is the best known and is the one retained in this paper.

HISTORY

Hylemyia cilicrura is probably of European origin. In North America the first record was that of Fitch (1856), who found the fly on wheat heads and described it under the name *Hylemyia deceptiva*. Riley (1869) discovered the larva attacking corn in New Jersey and named the fly *Anthomyia Zeae*, but nine years later (Riley, 1878) he called it *Anthomyia angustifrons* Meigen when he found the maggots feeding on locust eggs in Kansas and other western States. It was reported that ten per cent or more of

[2] Dates in parenthesis refer to *Bibliography and Literature Cited*, pages 1025 to 1037.

these locust eggs were destroyed in this way. Later, Jack (1886) found the maggots destroying field beans in Canada. At intervals since that time the pest has suddenly appeared, destroying bean seedlings and injuring many other crops both in the United States and in Canada.

During the last few years *H. cilicrura* has once more become active in the New York bean fields, after a period of scarcity covering many years. Since 1914 moist weather conditions have tended to augment the normal number of flies. The injuries caused by the maggots of this species reached a maximum in 1917, but since that time there has been a gradual decrease in the amount of damage, and in 1919 and 1920 the loss due to the insect was hardly noticeable.

DISTRIBUTION

The seed-corn maggot has been found in many parts of the United States and Canada. It has been reported from nearly every State, from Maine to Florida and westward to the Pacific. In Europe, reports of its presence in Austria, Germany, Italy, England, and France may be found. It has been reported also from Hawaii.

Chittenden (1916) states that the species *cilicrura* causes much of the loss in the States south of New Jersey which is credited to the cabbage maggot, *Hylemyia* (*Phorbia*) *brassicae* Bousché, and to the onion maggot, *Hylemyia antiqua* Meigen (*Phorbia ceparum* Meade). Chittenden believes also (1909) that some of the work on the Pacific Coast attributed to *Hylemyia planipalpis* Stein may be due to *H. cilicrura.*

FOOD PLANTS

Hylemyia cilicrura has a wide range of food plants, according to Chittenden (1902) and other writers. Among the commoner of these may be mentioned beans, peas, lettuce, corn, cabbage, cauliflower, beets, turnips, radishes, seed potatoes, sweet potatoes, domestic garlic, crimson clover, onions, and hedge mustard. Whelan (1916) reports the maggot as breeding in fresh manure, in clover and alfalfa sod, and in rotting clover stems. Tucker (1917) reports *cilicrura* injury on tomatoes and cauliflower, and says that the larvae were found developing in decomposed cotton seed. Garman (1904) found the insect in young hemp plants. Pettit (1910) mentions pumpkin, cotton, orange, artichoke, and strawberry as hosts. Parks[3] bred *cilicrura* from maggots in the "bulbs" of wheat. Howard (1900) states that the fly has been bred from human excrement. Riley (1878) found the maggots feeding on locust eggs.

The attraction of the insect for decaying matter has been recognized by many writers. Chittenden (1902) cites, as an example of this, the finding of the larvae in tineid galls on poplar trees. Quaintance and Jenne (1912) found the flies appearing in cages where decaying plums

[3] As stated in a general discussion reported in the *Journal of Economic Entomology*, vol. 9, p. 133, 1916.

were used in rearing the plum curculio. Johannsen (1911) thinks the species is attracted by decaying matter in the soil. Berger (1908) found the insect working in cut surfaces of seed potatoes that showed decay. Schoene (1916) has often bred the insect on cabbage, and believes the species is attracted to that plant by decomposition in parts of it. Blackman and Stage (1918) bred the species on a decaying root of larch.

The insect has been reported also in Europe. It was found on sea kale in England, and Ritzema Bos (1890) reported finding the species *platura* (which, as already noted, is a composite of *cilicrura* and *trichodactyla*) on human excrement, on asparagus, on leek (*Allium porrum*), and on shallot (*A. ascalonicum*). More recently this species has been discussed, under the name *Chortophila cilicrura*, as a pest of rye and corn in Silesia (Oberstein, 1916). Kornauth (1916) reports *trichodactyla* as injurious to beans in Moravia.

Under field conditions in western New York during the progress of the present study, larvae of *Hylemyia cilicrura* have been found in beans, peas, corn, seed potatoes, and alfalfa roots. Baits of decaying materials were placed near the laboratory, and later examination showed the following to contain maggots: cabbage, bean pods, bean vines, grass stems, clover roots, and clover stems. Two larvae have been found in mustard growing near a bean field, and two flies were bred from larvae taken in late summer in the roots of quack grass (*Agropyron repens*). The species has been reared also from pupae found in a pile of rich soil that had been taken from beneath decaying stumps. The writer has never bred the fly from manure.

From these data it may be seen that the list of known hosts is both large and varied, including not only healthy and decaying vegetable tissue, but also animal tissue. It is probable that this list is far from complete.

The first flies taken each spring have been found by sweeping old wheat fields, and the writer believes that wheat, oats, and possibly other grains, may constitute important late-season hosts; but as yet sufficient data are not available for proof of this. Mature females of the second brood, taken in July, were numerous near sod and quack grass, and these also may be common winter hosts of the insects.

NATURE OF INJURY TO BEANS

The larvae of the seed-corn maggot may feed on three parts of a bean seedling—the plumule, the cotyledons, and the radicle. The injury to each part of the plant is here discussed separately.

Injury to the plumule

When the small larva locates a source of food in a sprouting bean, it usually crawls between the cotyledons, or seed leaves, and feeds on the two leaflets of the plumule and on the small bud of the growing tip between

them (Plate LXIX, 4, and fig. 86, A). This vegetative part of the plant may be entirely eaten away so that when the seedling comes above ground

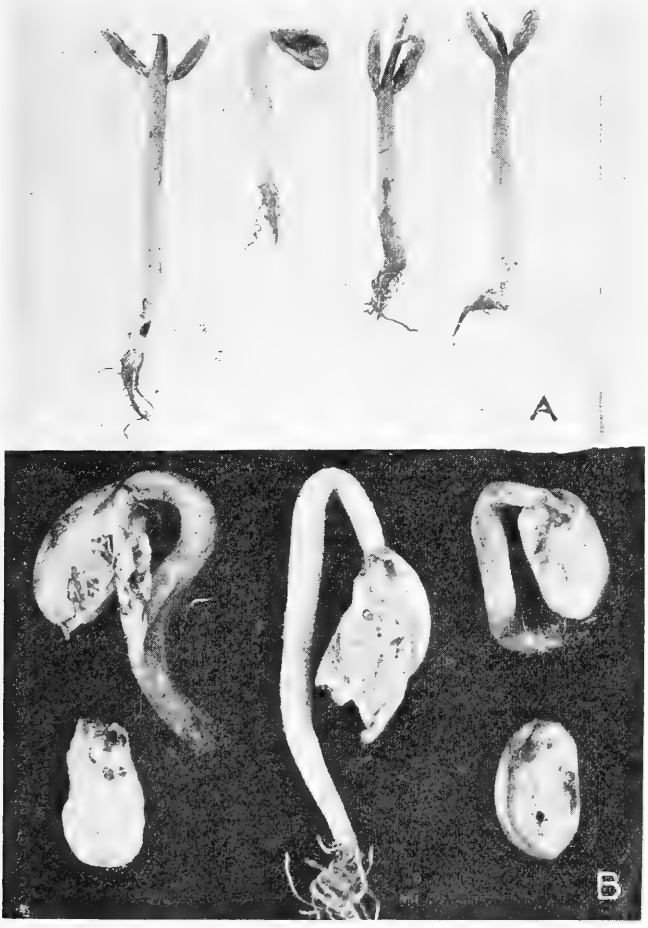

FIG. 86. INJURY BY HYLEMYIA CILICRURA

A, Types of injury in bean seedlings. B, Injured bean plants known as *snakeheads*, showing the result of feeding by the seed-corn maggot

only the cotyledons remain. This stunted form of plant is known to bean growers as a *snakehead*, or *baldhead* (fig. 86, B). Usually a snakehead shrivels up and dies, but occasionally one succeeds in producing accessory

buds and in developing leaves and a few flowers (fig. 87, A). At harvest time a plant of this type is found to bear few if any pods and is still a dwarf plant (fig. 87, B). The formation of snakeheads is the severest form

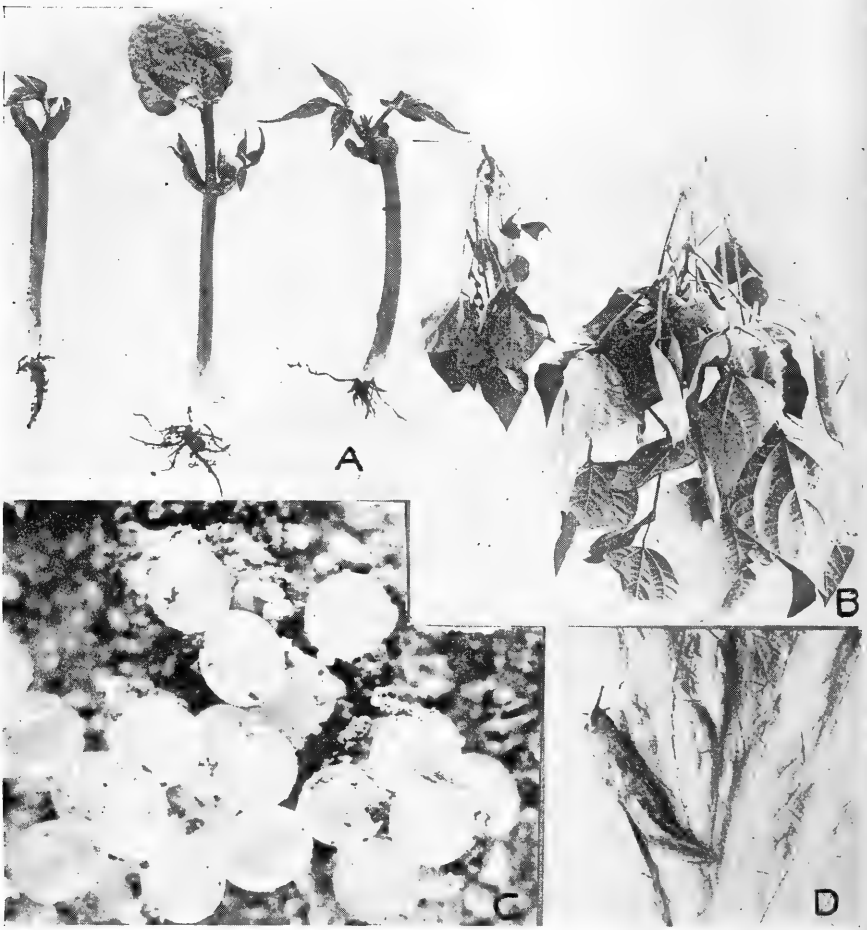

FIG. 87. RESULT OF WORK OF HYLEMYIA CILICRURA, AND EGGS AND ADULT OF AGRIOLIMAX AGRESTIS

A, Snakeheads putting out a new growth of small leaves. B, Two bean plants in late summer; the one on the left came from a snakehead, while the one on the right is a normal plant
C, Eggs deposited in the soil by *Agriolimax agrestis*, × 5. D, The field gray slug on a cabbage leaf, slightly reduced

of injury to the bean caused by the seed-corn maggot, and in some fields the writer has found 75 per cent of the plants to be thus deformed.

If the maggot feeds on the leaf tissue of the plumule but does not destroy the growing tip, a thrifty plant may still result. The first two leaves may be misshapen and ragged, but new leaves are soon produced to take their places.

Injury to the cotyledons

Often a larva does not injure the cotyledons until it has fed on the plumule. Its entrance into a cotyledon is thru a hole made in the side, and the maggot usually hollows out the fleshy interior until little more than a shell remains. The maggots are often carried above the ground concealed in the cotyledons, and a single plant may have eight or even more hidden in these two seed-leaves. Damage to the cotyledons alone is not a serious handicap, as these are of little use to the plant after the true leaves have been formed.

Injury to the radicle

When a seed germinates so quickly that the cotyledons are pushed above the ground before any maggots locate the plant, the radicle may be attacked. The larva makes a small hole for its entrance and then mines upward thru the fleshy tissue of the stem. This injury is not serious, as the course of the maggot is thru the pith and it seldom disturbs the vascular tissue. In 1917 the writer observed a field near Batavia in which the beans were planted very deep. Soon after planting, a period of dry weather baked the top soil solid. The beans grew until they reached this upper impenetrable surface layer, and then they were bent over. Many maggots were found in the stem of each plant.

LOSS CAUSED

The year 1917 was a serious one for New York bean growers, because of the continued rains and the prevalence of maggots during the planting time, in June. In five townships of Genesee County the loss of seed attributed to *Hylemyia cilicrura* was estimated at $15,000. In Erie County the loss on 10,478 acres was said to be 40 per cent. In Monroe County from 50 to 75 per cent of the beans on 16,000 acres were destroyed, while in Orleans County one-fourth of $96,000 worth of seed was wasted. Many growers had to plant their beans two or three times, and one grower, who reseeded twice before getting a stand, estimated his loss for seed at $300. Similar injuries to bean crops were reported from New Jersey, Pennsylvania, Michigan, and Canada. At intervals in the past this insect has appeared thus suddenly and unexpectedly, has seriously damaged beans, corn, and other crops for a few subsequent years, and has then gradually disappeared for a time.

DESCRIPTION OF STAGES

The egg

The chorion, or outer covering, of the egg (figs. 88 and 89, C) is white, glistening, and marked with longitudinal furrows. Similar cross-furrows connect the longitudinal ones, cutting off irregular areas about twice as long as their width. One end of the egg is rounded and the other is rather bluntly flattened. Two prominent ridges, starting at either end of the flattened part, meet at a point about one-fourth the length of the egg. When the larva emerges, the chorion splits near these ridges. The length of the egg is about 1 millimeter (1/25 inch).

FIG. 88. EGG OF SEED-CORN MAGGOT, × 30

The larva

The full-grown larva (Plate LXIX, 2, and fig. 89, D) is white, and is largest at the caudal end, tapering anteriorly. In the early stages it is slender and almost conical, but as it nears the time for pupation it becomes shorter and almost elliptical in form. The first segment bears a pair of black, hooked jaws which may be extended and retracted. The anterior spiracular process is heavily chitinized and bears six or seven lobes. The posterior spiracles are small and consist of three slitlike openings with toothed edges. These spiracles, which are the external openings of tracheae running lengthwise thru the body, may be found on the flattened caudal end of the larva. This flattened, almost truncate, segment bears seven pairs of fleshy tubercles. The length of the larva is from 6 to 7 millimeters ($\frac{1}{4}$ inch).

The puparium.—The puparium (figs. 89, A, and 90) is brown in color and elongate-oval in outline. The puparium is the cast skin of the last molt of the larva, and so shows many larval characters. The anterior spiracles are present on the anterior part of the puparium and still show six or seven lobes. The fleshy tubercles on the caudal end of the body also remain but are less prominent. The length of the puparium is about 4 to 5 millimeters ($\frac{1}{6}$ to $\frac{1}{5}$ inch).

The adult

The male (Plate LXIX, 1, and fig. 89, B).—The body color of the adult male is greenish gray, with the legs darker and the antennae black. The entire body bears many black bristles. Faint dark lines run lengthwise on the dorsum of some specimens, and a prominent black line runs along the middle of the dorsal side of the abdomen. The main distinguishing character of the species is a row of regularly arranged bristles on the tibia of the hind leg (Plate LXIX, 3). This separates the species *ciliicrura*

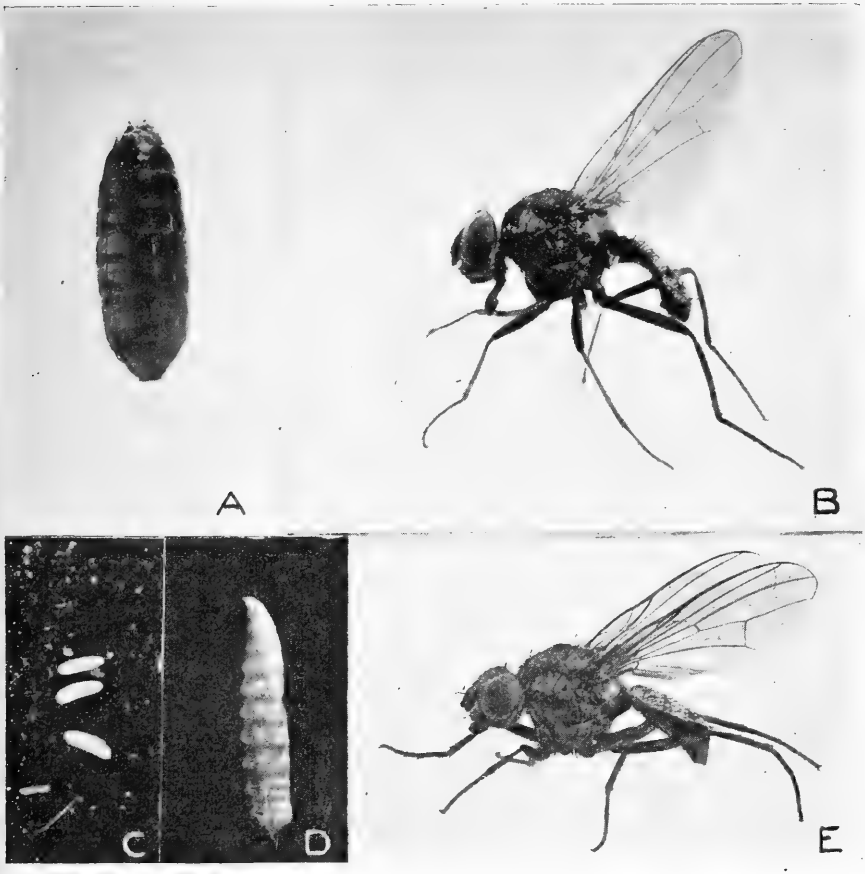

FIG. 89. THE SEED-CORN MAGGOT, HYLEMYIA CILICRURA

A, Puparium, × 8. B, Parent fly, male, × 10. C, Eggs, on dirt, × 6. D, Larva, × 5. E, Parent fly, female, × 10

from *brassicae* and *antiqua* (*ceparum*), with which it is often found associated in the field. In *brassicae* there is a tuft of fine setae at the base of the femur, which is lacking in *cilicrura*. In *trichodactyla* the middle metatarsus bears long hairs on the upper side, which are lacking in *cilicrura*. The length of the adult male of *cilicrura* is about 5 millimeters ($\frac{1}{5}$ inch).

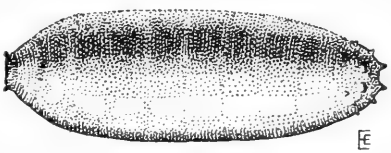

FIG. 90. PUPARIUM OF SEED-CORN MAGGOT, × $5\frac{1}{3}$

The female (fig. 89, E).— The female of *cilicrura* is similar to the male, but

the abdomen is pointed instead of rounded and the bristles on the body are fewer and shorter. The female lacks the prominent fringe of hairs found on the tibia of the male, and is harder to distinguish from related species. In *brassicae* the pre-alar bristle is as strong and as long as the first dorso-central one, while in *cilicrura* and *antiqua* it is only about half as long. In *antiqua* there are two nearly equal setae on the anterior (outer) side of the middle tibia, while in *cilicrura* there is usually but one. The species *antiqua* is ordinarily larger than *cilicrura*. The length of the female of *cilicrura* is 5 millimeters ($\frac{1}{5}$ inch).

LIFE HISTORY AND HABITS

The egg

There is little in the literature regarding the egg-laying of *Hylemyia cilicrura*. Whelan (1916) reports that the fly usually places its eggs either on the stems of plants just as they come thru the soil, or on decaying vegetable matter. Howitt (1911) states that the eggs are deposited on decaying matter in the soil. Lugger (1896) was able to bring about the deposition of eggs by flies in captivity, but he believed the eggs to be sterile for he failed in his attempts to rear flies from them. Chittenden (1909) mentions an instance in which decomposing crimson clover that had been plowed under attracted flies as a place for oviposition.

Period of incubation

In July, 1917, at Perry, New York, the length of the egg stage under very moist conditions was between 24 and 48 hours. Very few eggs were found and the exact time of oviposition was in doubt.

In 1918 eleven first-brood eggs under observation hatched in an average of 66 hours, as shown in table 1. There was a wide variation, from 41 to 91 hours, and many eggs, the exact hatching time of which could not be noted, hatched within these limits. Eggs were kept in petri dishes on moist blotting-paper or damp earth.

TABLE 1. LENGTH OF THE EGG STAGE IN 1918

Number of eggs	Time of deposition	Time of hatching	Length of stage (hours)
3.....	May 23, 3 p. m.....	May 27, 9.30, 10, 10, a. m.....	90.5, 91, 91
4.....	May 25, 4 p. m.....	May 27, 9, 10, 10, 11.30, a. m...	41, 42, 42, 43.5
4.....	May 25, 3 p. m.....	May 28, 9.30, 10, 10.30, 10.30, a. m.....	70.5, 71, 71.5, 71.5

Average, 66 hours.

In 1919 notes were taken on the period of incubation of 28 eggs on moist earth. The average for these was 2.8 days, with a range from one to five days. Four eggs kept on dry blotting-paper in a petri dish required between three and four days. One egg, deposited on June 4, did not hatch until June 17, but this is the only instance of so long a period of incubation.

Place of oviposition

The insect is strongly attracted to moist and decaying material as a place for oviposition, but under some conditions the flies will place their eggs on dry material, as the following experiment shows. On June 4, 1919, many flies, taken by sweeping, were placed in a cage with a flower-pot containing dry bean stems and dry soil. This pot was kept dry until the flies died, after which it was moistened in order to see whether a new lot of flies would develop. On July 3 one fly was found in the cage, and on July 8 two more were found. In another cage the same conditions prevailed except that the jar was moist during the entire experiment. Four flies were found in this cage on July 3, and eight more on July 8.

In the field, eggs have been found around decaying bean pods and vines and around rotting cabbage. The writer has spent a great deal of time in looking for eggs on freshly plowed ground where mature flies were seen in large numbers, but has succeeded in finding only a few in such locations. Two eggs were found on newly turned soil and one was discovered in a crevice in a recently disked field. Egg-laying was induced by throwing water on the parched and cracking ground near the laboratory at a time when the flies were numerous. Eight eggs were found on top of the ground in one of these spots within two hours after it was thus moistened, and, in all, about one hundred eggs were obtained in this way.

Whelan (1916) says that the maggots of *H. cilicrura* are sometimes found in fresh manure. The writer, however, has not seen the larvae in manure, nor has he been able to bring about oviposition on manure. On June 5, 1919, flower-pots containing fresh cow, horse, hog, and hen manure were placed in a cage containing many adults of *cilicrura* that had been taken in the field. When these pots were examined later, no eggs could be found, and no flies ever emerged in the cage. On June 3, 1919, flies were placed in a large cage containing one flower-pot of manure of different kinds and another filled with decaying bean vines and grass sod. After the flies were all dead, the pot of manure was moved to another cage. No flies emerged from this pot. In the cage containing the pot with the decayed beans and grass sod, thirteen flies emerged. This apparently shows the insects' preference for decaying beans and clover rather than for animal manure, as a place for oviposition. Many times fresh manure found in fields where the flies were abundant has been placed in cages, but no flies have ever emerged. Furthermore, the flies have not been found in abnormal numbers around either manure piles or fresh manure dropped along the road.

Is it possible that manure has an attraction for the maggots developing from eggs deposited in the soil, which leads them to use it as a secondary host?

In cages, eggs of the first brood have been found singly as a rule, tho they have been found occasionally in groups of from two to five, in some cases side by side and in other cases piled on one another irregularly. When first-brood flies taken in the field were placed in cages, eggs were deposited on decaying mustard stems, on stems and roots of grass, on old bean pods and vines, and on cabbage stumps. Some eggs were found a so on the surface of the ground, and some in the top inch of dirt. A few were attached to the side of the flower-pot, both above and below the soil line. Eggs of the second brood were deposited by flies in captivity on top of the soil and in the dirt itself.

Number of eggs

The writer has not been able to bring about oviposition by flies reared in captivity, and accordingly he could not determine the exact number of eggs deposited by a single female. The following may be mentioned as typical examples of many dissected specimens. On May 27, 1918, 87 eggs, of which 25 were almost fully developed, were found in a dissected fly. On May 15, 1919, two flies were found with nearly mature eggs, one containing 30 and the other 48. In 1920 two flies were found containing 83 and 64 eggs, respectively, on May 7; and on May 19, five flies contained, respectively, 56, 25, 37, 85, and 72 eggs. It is believed that all the eggs in an insect mature at about the same time and that oviposition is completed within a few days. From these data it seems possible that a female may deposit 80 or more eggs, but the number may often be much smaller.

Time of oviposition

Since it is from the eggs of the first brood of flies that the maggots so injurious to growing crops are produced, special study has been given to this generation. Very little is known of conditions in 1917, as life-history studies did not begin until June 22. In 1918 adults were found containing well-developed eggs on May 9, and, tho some eggs were no doubt deposited by May 15, most of the eggs of the first brood were deposited between May 23 and June 1. Eggs of the second brood were deposited during the first half of July.

In 1919 eggs of the first generation were mostly deposited from May 20 to June 15, with the maximum deposition occurring about June 4. Second-brood flies were ready to oviposit between June 25 and July 4. Since a few flies were captured on September 13 and 15 whose abdomens contained immature eggs, it seems possible that a few eggs may have been deposited as late as October. However, these flies may hibernate, which would explain why a few flies with well-developed eggs are found in early May, several weeks ahead of most of the first brood.

The season of 1920 varied little from the two preceding years. The first flies were found on May 7, some containing eggs that were partly developed. Most of the eggs of the first brood were deposited during the first week of June. Eggs of second-brood flies were deposited early in July. The relationship between the time of oviposition and the dates of bean planting is discussed later (page 972).

The larva

Length of larval stage

The average length of the larval stage for eight specimens of *Hylemyia cilicrura*, which had been bred in vials in a field cage at the Perry laboratory in 1917, was 10.4 days, with a variation from 8 to 12 days. The data are given in table 2:

TABLE 2. BREEDING DATA FOR EIGHT FLIES REARED IN 1917

Date of hatching	Length of larval stage (days)	Date of beginning of pupal stage	Length of pupal stage (days)	Date of emergence of adult	Time from egg to adult (days)
July 17	12	July 29	20	August 18	32
July 17	11	July 28	14	August 11	25
July 18	12	July 30	11	August 10	23
July 25	8	August 2	10	August 12	17
July 25	10	August 4	12	August 16	22
July 26	9	August 4	12	August 16	21
July 26	9	August 4	16	August 20	25
July 26	12	August 6	15	August 21	27
Average	10.4	.....	13.7	.....	24

In June, 1919, the average larval period in the case of twenty-one first-brood maggots bred in the laboratory at Perry, was 9.4 days, with a range from 7 to 12 days. Specimens bred in the field cages required about two days more.

Habits of the larva

The larvae of *Hylemyia cilicrura* are instinctively internal feeders. When they hatch, the small larvae crawl thru the crevices of the soil in search of food. In this search they show a preference for material that is beginning to rot, and they are always most numerous in decaying beans. Seventeen maggots were once found in a slightly decomposed bean, and seven to ten is not an uncommon range. They may be found in sound

beans also, tho a sound seed rarely contains more than two or three. Beans that are entirely decomposed have no attraction for the insect.

In order to test the ability of a maggot to find its bean host, ten newly hatched larvae were placed on top of the soil in large vials, in July, 1917, and an unsoaked bean seed was placed at the bottom of each vial. Eight of the ten maggots found the bean and were reared to adults.

The pupa

Time spent in puparium

In the summer of 1917, the length of the pupal stage of eight specimens was found to be 13.7 days, as shown in table 2. The average length of the pupal stage of seventeen additional specimens, carried thru in the outdoor cage in July, was 12.8 days, the time varying from 10 to 14 days. In June, 1919, the average time required for nineteen pupae was 10.2 days, with a range from 8 to 14 days. The time required in a field cage, from the hatching of the egg until the emergence of the adult fly, was found to be 22.7 days for forty-five specimens, with a range from 16 to 27 days. Allowing 10 days for the larval stage, this would make the average pupal period 12.7 days. Cages have been examined for puparia tending to show a lengthened pupal period, but cases of retardation, such as those noted by Schoene for the closely related cabbage maggot (*Hylemyia* [*Phorbia*] *brassicae*), have not been observed. In 1918, however, the rainfall at Perry during July and August was far below normal (table 6, page 971), and in the fall of that year only one fly of a possible third brood was seen. In both 1917 and 1919, third-brood flies were numerous. The absence of a third brood in 1918 might have been due to a lengthening of the pupal period of the second brood caused by the high temperature and low rainfall.

Place of pupation

Puparia of *Hylemyia cilicrura* are usually found near the surface of the ground, a short distance from the place of larval feeding. They are occasionally found as deep as six inches below the surface, but ordinarily not more than three inches below. In bean fields they are often seen within a few inches from the plant food of the larva.

The adult

Emergence

The emergence of what are believed to have been second-brood flies reached its height at Perry, New York, on July 13 and 14, 1917. The flies continued to appear in the rearing cages until about August 1. Flies reared from eggs deposited, no doubt, by this brood and hatching about July 25 and 26, produced, late in August and September, what was possibly a third brood. It is believed that an entire brood of flies was

missed in that year, owing to the delay in opening the laboratory. In that year the spring was very late and the rainfall was heavy thruout June and July.

In 1918 a few females with well-developed eggs were found on May 9. It is not definitely known whether these flies hibernated as adults or were very early specimens of a main brood which came later. Judging from the number of flies taken in the field, the maximum emergence of first-brood flies occurred between May 23 and 26. Second-brood flies appeared in the cages from June 26 to July 5. After July 23 only one fly was found. This was a male, taken on August 26. In that year there were apparently only two broods. The adults came out early in the spring, but, as a result of the hot, dry weather at Perry in late July, either the flies died or the development of the stages of the following brood was retarded.

In 1919 a few flies were found after May 15, but it was not until June 2 that they were at all abundant. They could stil be found easily on June 9, and occasionally until June 17. Most of the females deposited their eggs during the first week of June. Second-brood flies appeared in the cages from June 18 to July 3, with the maximum emergence about June 25. The hot weather of mid-July must have proved fatal to most of the flies, for they disappeared entirely and no more were seen until September 9. Then, for a few days, flies of the third brood were taken. In 1919 there were apparently three broods, or at any rate two and a partial third. The data leading to this conclusion are given in table 3:

TABLE 3. SUMMARY OF RECORDS TENDING TO SHOW THE NUMBER OF BROODS IN 1919

Date		Observations
May	15	3♂, 6♀, taken by sweeping; 2♀ containing well-developed eggs
	20	A few flies taken in an old wheat field
	27	Flies still scarce
	29	2♂, 3♀, taken; eggs small; few flies seen; weather cold
June	2	Flies plentiful; eggs in females ranging from partly developed to mature
	4	Eggs found on decaying material in cages; females in field containing a few mature eggs or no eggs
	9	Fewer flies; abdomens empty Small maggots found in beans planted June 2
	11	3♀ taken containing no eggs; abdomens collapsed
	19	First of second-brood flies emerged in cages
	20	13 second-brood ♀ from field examined; eggs undeveloped
	25	Many second-brood flies coming out
July	3	A few second-brood flies still coming out
	15	Weather hot; few flies
	26	No flies seen; flies in cages dead, probably owing to hot weather
Sept.	13	1♂, 3♀, taken on ground plowed for wheat; eggs immature
	15	1♂ taken

In 1920 the first flies were found on May 7, and during periods of warm weather they continued to emerge in numbers until the first of June. Most of the eggs of this brood were deposited between May 25 and June 5. Weather conditions in July of that year were more favorable than in 1919, and flies lived in the cages until the first of August.

Dates of emergence vary greatly at different altitudes. Flies have been found in abundance, a week or more before the Perry emergence, at places ten miles from Perry where the elevation is much less. The bean laboratory was located on what is said to be one of the highest points between Lake Erie and the Genesee River, its elevation being 1400 feet. Data obtained at Perry, therefore, while holding true for much of the western New York bean-growing section, are probably later than for most parts of the State. The opening of spring at Perry is at least a week later than it is at Ithaca.

The time of emergence of *Hylemyia cilicrura* is dependent largely on temperature. If there are several warm days early in May, some flies will appear. If such a warm period is followed by colder weather, additional flies may not be found for a week or two, or until the temperature has again moderated.

Length of life

Adults of *Hylemyia cilicrura* have lived in cages for from 2 to 44 days. In 1920 nine flies under observation lived for an average of 26 days. Without food, life is short, but in cool weather the flies will live for many days in moist cages if they are supplied with sweetened water. The time in this period when eggs are deposited is not well known; but from the fact that adults with immature ovaries are normally found for many days before mature specimens appear, it is probably toward the end of the adult life. Many flies were taken by sweeping in the field on May 20, 1920, at which time most of the females dissected contained immature eggs. Flies taken at this time were placed in cages, and deposited eggs between June 1 and June 6. Apparently, then, the length of the preoviposition period is about two weeks.

Habits

The author's inability to obtain eggs from flies reared in captivity has already been mentioned. Molasses, sugar water, and decaying material were placed in cages, but all failed to supply suitable conditions. A large cage, six feet square, in which beans, cabbage, and mustard were growing and which contained decaying material also, failed to give any better results. Flies were attracted in large numbers by sugar water and molasses. In the field many flies were found in bait pans containing a mixture of molasses, water, and sodium arsenite.

In the spring the flies are attracted to moist, newly plowed ground. They crawl deep into the crevices of the soil, stopping occasionally to lap

up a drop of moisture as they find it. When the flies are moving about in this manner, the wings are overlapped on the back and are thus out of the way. Twelve flies have been counted in three feet of furrow, and forty-two were seen in a square yard. A count of the flies taken on new soil on May 27, 1918, showed fourteen mature females and one male. At this period or a little later, many flies may be taken by sweeping along the edges of fields and roadways. On June 18, 1918, many were caught in the tall grass at the edge of a field, a count showing about four males to every female. On July 8 there were forty-one males in a lot of forty-five flies taken by a roadside. It is apparent, then, that while the females are searching for places suitable for oviposition, the males may be found sunning themselves in grassy and weedy places. On sunny days, adults have been seen resting on mustard; and in the evening they are found on onion tops, kale, potato vines, daisy, and ragweed, and more rarely on other plants. Flies have also been observed hovering about a dead earthworm lying on the surface of the ground.

On warm days, or during the hotter part of the day, the flies are very active, crawling restlessly near the top of breeding cages; but in cold weather they move slowly over the dirt on the floor of the cage, or remain quiet in the cracks of the soil.

It was observed in the spring of 1919 that flies might be taken in the grass along roadsides, and in wheat and oat fields, before they made their appearance around plowed ground. It would seem, then, that as the egg-laying period approaches, flies have a tendency to come into the open and seek loose, moist soil. This is especially true if such soil contains, as an additional attraction, the decomposing roots of clover or quack grass.

HIBERNATION

The writer has little data on the hibernation of *Hylemyia cilicrura*. Cages have been placed in fields and meadows early in the spring, but no flies have emerged in them. Early in May a few flies with ovaries partly mature have been found. It is probable that these were early specimens of the subsequent first brood, which had wintered in puparia; but they may have been flies that had emerged late in the previous summer and had hibernated as adults. It has not been possible to keep flies that are taken in late summer, alive in cages thru the winter. The writer believes that the insects more commonly pass the winter hibernating as second-generation pupae, and emerge as flies from May 15 to June 1 of the next year. Such flies, taken in late May, had only partially developed ovaries and were fresh-looking specimens. In support of this pupal-hibernation theory, N. F. Howard[4] found *cilicrura* hibernating in the pupal stage in onions in Wisconsin, and Dickerson (1910) showed that from pupae of *cilicrura* placed in cages in November, flies would emerge early in May of the next year.

[4] As stated in a general discussion reported in the *Journal of Economic Entomology*, vol. 9, p. 133, 1916.

SEASONAL HISTORY

Adult flies of the first brood are found in the fields from early in May until the middle of June, and deposit their eggs on decaying material or on moist soil about bean-planting time, during the last of May or early in June. The maggots work in beans, corn, potatoes, or rotting vegetation, and emerge as second-brood flies in July. These flies soon disappear in normal hot, dry summers, but apparently they deposit eggs about decaying vegetable matter before they die. A few third-brood flies may appear in August and September, some of which may hibernate; but most of the flies taken in May of the next year are believed to come from the midsummer brood of pupae which overwinter.

CONTROL

Control measures for *Hylemyia cilicrura* may be classed either as artificial, such as seed treatment and the use of baits, or as cultural. The cultural methods involve studies of influential factors in the environment of the insect, and of practices used in growing the crop which may affect the extent of infestation by the maggots. The artificial methods are recorded first.

Artificial methods of control

The studies in artificial control that have been directed against *Hylemyia cilicrura* in the past have been concerned mainly with seed treatments and with the application to the soil of such materials as would either kill the maggots or act as repellents for the adult flies and thus prevent the deposition of eggs. Lintner (1882 a) suggests soaking the seed in gas tar or copperas to keep the maggots away, and Lugger (1896) says these materials work well on a small scale. Headlee (1913) tried solutions of corrosive sublimate, sulfocide, and potassium cyanide, in an effort to kill the maggots and prevent oviposition by the flies, but his results were unsatisfactory. Later (1918) he tells of trying strips of tar, and also of the application of sand treated with carbolic acid to the surface of the soil just after beans were planted. As a result of this treatment, a few more plants came up in the treated plots than in the checks. Still later (1920), Headlee found that a repellent effect on the maggots resulted from treating lima beans with coal tar and dusting them with ashes, lime, or tobacco dust. Chittenden (1909) suggests that carbolic acid might act as a repellent to the adult flies, and both he and Bruner (1910) advise the application of kainit, nitrate of soda, or sulfate or chloride of potash to the soil as a top dressing. In addition to discouraging oviposition, this practice is said to have the added advantage of stimulating plant growth.

While seed treatment and the application of insecticides to the soil may be of value when used in a small way, these practices are of doubtful importance as control measures on a field scale. An infestation of the

TABLE 4. EXPERIMENTS CONDUCTED AT PERRY, NEW YORK, IN 1917, ON SEED AND SOIL TREATMENT FOR THE SEED-CORN MAGGOT

Experiment	Material	Manner of application	Number of seeds planted	Date planted	Date examined	Number of seeds germinated	Number of snakeheads	Remarks
A_1	Hellebore	Drilled in	100	July 12	July 19	78	0	
A_1	Hellebore	Drilled in	50	16	23	20	7	
A_2	Hellebore	On seed	100	16	26	2	Hellebore mixed with cottonseed oil	
B_1	Iron sulfate	On seed	50	12	19	28	3	2 pounds in 1 gallon of water
B_1	Iron sulfate	On seed	100	16	23	2	1	Flour added as sticker; germination hindered
B_2	Iron sulfate	On seed	50	16	23	5	0	Poured on seed in row
C_1	Borax	On seed	100	12	19	0	0	No germination; radicle injured
D_1	Carbolic emulsion	On soil	50	16	25	22	0	No injury; growth slow
E	Kerosene emulsion	On soil	50	16	25	0	0	Seeds rotted by drench
F_1	Sulfocide (1–1)	On seed	100	12	19	12	0	Cotyledons decayed
F_2	Sulfocide (1–1)	On soil	50	12	19	43	0	Good stand
F_3	Sulfocide (1–1)	In row	50	12	19	45	0	Good stand
F_1	Sulfocide	On seed	100	16	23	22	6	Concentrated material; injury resulted
G_1	Lime-sulfur (1–1)	On seed	100	12	19	20	4	
G_2	Lime-sulfur (1–8)	On soil	50	12	19	35	0	
G_3	Lime-sulfur	In row	50	12	19	0	0	Concentrated material; beans injured
G_2	Lime-sulfur	On soil	50	16	23	17	1	Concentrated material; beans injured
H_1	Dry bordeaux	In row	50	12	19	0	0	Discolored seed coat; germination delayed
H_2	Dry bordeaux	On soil	50	12	19	37	1	Good stand
H_1	Dry bordeaux	On seed	100	16	23	58	1	Good stand
H_2	Dry bordeaux	In row	50	16	23	43	1	Good stand
H_3	Dry bordeaux	On soil	50	16	23	45	1	Good stand
I_1	Creosote	On seed	100	12	19	0	0	Beans rotted
J_1	Quassia solution	On seed	100	16	23	30	3	Normal spray solution, hop-aphis strength
J_2	Quassia solution	In trench	50	16	23	17	2	
K_1	Black-leaf-40 (1–100)	On seed	100	12	23	0	0	Seed decayed
K_2	Black-leaf-40 (1–100)	On soil	50	16	23	12	2	Slow growth
L_1	Sulfur	In trench	100	16	23	28	7	
M_1	Tobacco dust No. 1	On seed	50	16	23	10	1	Slow growth
M_2	Tobacco dust No. 2	On seed	50	16	23	1	0	Slow growth
R_1	Scalecide (1–15)	On seed	100	16	23	25	8	
R_2	Scalecide (1–15	On soil	50	16	23	20	4	
	Check		100	12	19		4	
	Check		100	12	19		8	
	Check		50	12	19		4	
	Check		100	12	19		3	
	Check		100	16	23		11	
	Check		100	16	23		8	
	Check		100	16	23		4	
	Check		100	16	23		2	

seed-corn maggot cannot easily be predicted; its first indication to the grower is usually the discovery of the maggots in beans that have failed to germinate. Since this is true, an efficient repellent or seed treatment would have to be used every wet year, which would make the cost for material and labor very high. Furthermore, it is difficult to find a material which does not injure the seed and yet has a killing or repellent effect on the insect. Maggots usually enter the bean between the cotyledons, and therefore, after the seed coat, which bears the treatment, is broken or cast off by the swelling of the seed, the tender plumule is again left unprotected.

The writer has tried various materials as control measures, on a small scale, in the hope of finding something suitable for larger tests. The results of these experiments are recorded in table 4.

In the experiments reported in table 4, the materials were placed either on the seed coat, on top of the soil, or in the row with the planted seed. These experiments were located in fields where bad infestations of maggots had just been found and where the flies were very numerous. Infestations were not large, however, as the plantings came between broods. Dry bordeaux mixture seemed the most promising of the materials tested, but on the whole the results of experiments in 1917 were not encouraging.

In 1920, seed- and soil-treatment experiments were again conducted. A part of the experimental field which had not been under cultivation for several years, and which was covered with quack grass, was plowed, and the experiments were started here on June 4. At that time many females of *H. cilicrura* were mature and had been depositing eggs for several days. Beans were planted, following a rain of 0.25 inch, on June 3. It was noted that the flies had been more numerous on this part of the field than on the other parts which had been previously under cultivation, showing the attraction of the species to turned-under quack grass as a place for oviposition. Snakeheads, the evidence of maggot attack, were much more abundant here than in the main part of the field when counts were made on June 22. The results of the experiments of 1920 are given in table 5.

None of the materials tested in 1920 gave promise of success in practical use. While in a few cases the number of injured plants was reduced, in no case did the seedlings entirely escape harm. Taking into consideration the difficulty of predicting infestations of the seed-corn maggot, it seems to be unwise to rely on control measures of this type in New York.

The bait of sodium arsenite, water, and molasses, which was tried against the onion maggot by Sanders,[5] was tested against *H. cilicrura*. On June 21, 1917, the material was sprinkled on the soil with a whisk broom, and pie tins containing it were placed in a row across the field. Flies were very numerous in this field and the second planting of beans had just been made, the first seeding having been destroyed. On the morning of June 22, twenty-nine flies were found in the pans, together with many beneficial

[5] As stated in a general discussion reported in the *Journal of Economic Entomology*, vol. 8, p. 89, 1915.

TABLE 5. EXPERIMENTS IN 1920 ON CONTROL MEASURES FOR THE SEED-CORN MAGGOT

Experiment	Material	Manner of application	Number of seeds planted	Number of seeds germinated	Number of snakeheads	Number slightly injured	Per cent of beans injured		Remarks
							In relation to those germinated	In relation to those planted	
Check			50	35	5	2	*29*	*14*	
A	Sulfur	In row	100	58	16	5	36	21	
B	Sulfate of potash	In row	100	52	14	6	38	20	
C	Calcium cyanamid	In row	100	23	4	1	21	5	Burning resulted
D	Nitrate of soda	In row	100	5	2	1	60	3	Burning resulted
Check			50	39	7	1	*20*	*16*	
E	Acid phosphate	In row	100	58	16	2	31	18	
F	Floats	In row	100	68	12	5	25	17	
G	Ammonium sulfate	In row	100	14	2	0	14	2	Injury resulted
H	Ground limestone	In row	100	71	7	3	14	10	
I	Nitrate of potash	In row	100	28	7	0	25	7	Growth slow
Check			50	39	8	0	*20*	*16*	
J	Dried blood	In row	100	40	10	1	27	11	
K	Gypsum	In row	100	68	21	2	33	23	
L	Dry bordeaux	In row	50	36	8	0	22	16	
Check			50	35	10	5	*42*	*30*	
M	Tobacco dust	In row	100	68	14	4	26	18	
N	Kerosene and lime	On soil	100	39	3	0	7	3	Growth delayed
O	Carbolic emulsion (1–20)	In row	100	50	3	2	10	5	
P	Tarred sand	On soil	100	41	0	2	5	2	Injury resulted
Q	Arsenate of lead (2–50)	On seed	100	66	5	3	12	8	
R	Bordeaux paste (4–4–50)	On seed	100	66	2	2	6	4	
S	Lime-sulfur (1–20)	On seed	100	65	6	1	9	7	
Check			100	65	5	4	*14*	*9*	
T	Carbolic and lime	In row	100	60	6	1	8	7	
U	Creosote and lime	In row	100	19	2	0	10	2	Injury resulted

carabid beetles. No dead flies were seen in the field outside of the pans, and later, when the beans came up, there was no reduction in the number of snakeheads near the pans. Pans were placed in other fields, and, tho many flies were captured, no great benefit was noticeable when the beans were examined two weeks later.

Before planting was done in this field, which was very wet, the seed was drenched with kerosene. Eight days after planting, the counts showed 49 maggot-infested seeds out of 110 that were examined. When the seed was treated overnight with carbon disulfid, 17 out of 57 beans contained larvae of *H. cilicrura*. A check had 28 infested seeds in 50. Altho neither material injured the germination of the seed, there was little if any repellent effect produced.

Beans were treated also with arsenate of lead in the form of a strong paste. This was allowed to dry and the seed was then placed in the ground with a bean planter. The poison so injured the seed that only about 15 per cent germinated. A check showed an 85-per-cent stand.

Neither seed treatment nor other artificial control measures have given promise of success. No satisfactory material has been found, and nothing that looks promising for tests on a large scale has been discovered.

Natural and cultural methods of control

There are many factors bearing on the presence or the absence of *Hylemyia cilicrura* in a field. Some of these are discussed in the following pages, and practices which are in the nature of preventives are pointed out.

Moisture and temperature as factors in the life of the seed-corn maggot

Hylemyia cilicrura has been found to be a serious pest in New York when the early summer is rainy. This increased injury in moist seasons is apparently due to the tendency of the cultivated hosts to decay in the wet soil, thus becoming attractive to the flies as a place for oviposition. It seems probable, also, that maggots already in the soil feeding on other decaying vegetation, are attracted to the beans when they begin to decay.

In June of 1916 and also of 1917, the rainfall far exceeded the normal. In 1917 the June rainfall (6.4 inches) was more than twice the monthly average for the previous twenty years, and the damage from *H. cilicrura* was severe in all the bean-growing sections of the State. July of that year was rainy also, and thruout that month flies could be taken easily, altho normally they are scarce at that season. The years 1918, 1919, and 1920 were nearly normal, and the loss was slight. In table 6 are given data from the United States Weather Bureau at Rochester, New York.

In periods of drought such as prevailed at Perry during July and August of 1918, flies are difficult to find. By July 22, 1918, only six flies of many hundreds were still alive in the cages, and on the following day not a fly

could be found in the field. On August 26 one male of *H. cilicrura* was taken, and this was the only fly seen in 1918 after July 22. The conditions at Perry in that year were abnormal, for this region suffered much more for want of rain than did the surrounding places. The reduction in the number of flies appearing at Perry in 1919 is possibly due to this prolonged dry period.

TABLE 6. TEMPERATURE AND MOISTURE RECORDS OF THE UNITED STATES WEATHER BUREAU AT ROCHESTER, NEW YORK, DURING THE SUMMERS OF 1917 TO 1920, INCLUSIVE

(Records of marked variations from the Rochester records found at Perry are given in boldfaced type)

Month	Mean temperature (Fahrenheit)					Rainfall (inches)				
	1917	1918	1919	1920	Normal	1917	1918	1919	1920	Normal
May	49.2°	61.7°	56.4°	55.8°	56.7°	3.16	1.75	5.20	0.78 **2.01**	2.94
June	62.8°	62.6°	72.8°	65.7°	66.1°	6.40	2.40	2.96	1.15	3.13
July	71.7°	70.2°	72.2°	67.8°	70.4°	4.23	2.70 **1.03**	3.40 **1.21**	2.93	3.09
August	69.0°	71.5°	67.8°	70.3°	68.3°	2.51	1.83 **1.34**	3.60 **5.70**	1.51	2.96

In July of 1919, the rainfall at Perry was again below normal, and the flies in the cages died rapidly after July 1. Between July 1 and July 20, the rainfall was only 0.67 inch, and the maximum temperatures for this period ranged from 65° to 96° F. After July 15 no flies were seen for two months and the specimens in cages all died. August of that year had nearly twice the normal rainfall.

The temperature early in the summer appears to have an influence on the abundance of *H. cilicrura*. In 1917 the mean temperature for May was 49.2°, which is several degrees below the average for the month and is the lowest recorded since 1871. The maggots and flies during that season were the most numerous in the history of the insect. June temperatures in 1917 also were lower than the normal, and had been each year since 1913.

H. cilicrura is an insect which in the past has been injurious for one year, or for a few successive years, and has then become of negligible importance for an indefinite period. This variation is undoubtedly connected to some extent with the moisture and temperature conditions of the early summer. Moderately low temperatures with an abundant rainfall in the spring appear to be favorable to the insect, while dry, warm weather during the summer is detrimental to its successful development. A succession of cold, wet years brings forth the insects in greatest numbers.

Relation of time of bean planting to time of oviposition

Eggs may be deposited by *Hylemyia cilicrura* near decaying vegetable matter in newly plowed or recently fitted soil before the beans are planted, while they are being planted, or even after planting. In rare instances a combination of these two possibilities may be found. When the eggs are deposited previous to planting, the maggots feed on decaying matter in the vicinity for a while, becoming nearly full-grown before they enter the bean seed; but when the eggs are deposited subsequent to planting, small larvae will be found in the beans within a few days after they are planted.

As examples of oviposition in the soil before the beans are planted, the following instances may be mentioned. In the experimental field at Perry, in 1919, one piece was plowed on May 14 and planted on May 28. When it was examined on June 5, many full-grown maggots were found. Allowing ten days for the larval period and two days for the egg stage, the eggs were probably deposited about May 24. A field that had been in alfalfa for several years was plowed for beans in May. Planting took place on June 6 and 7, and when the field was examined on June 12 the maggots present were ready to pupate. These maggots were hatched from eggs deposited probably about June 1. Maggots of about the same size were found in the old alfalfa roots.

As illustrations of egg-laying either at the time of planting or subsequent to it, the following examples are given. In 1919 a field of beans was planted on June 2. When it was examined on June 9, maggots a few days old were found. Flies were very common in the field on June 2 when the seed was drilled in. Beans were planted in a test plot on the experimental field on June 5. On June 10, when these were examined, some contained newly hatched maggots. In a field in Niagara County beans were planted on June 9. Small maggots were found feeding on the plumule leaves on June 14.

In the rainy year of 1917, when *H. cilicrura* could be found everywhere, fields were inspected late in June. Small and large maggots were found in the beans, pupae were in the soil, and flies with eggs in all stages of development were hovering over the ground. It is only late in the spring of very wet years that all stages can thus be found simultaneously. In more normal years the flies seem to appear in roughly defined broods, and the heavy oviposition of each brood does not extend over a period of more than a week.

From the foregoing data it is evident that a grower cannot be sure that maggots are not already working on other matter in the soil at the time when he plants his beans. Moreover, if mature flies are numerous at planting time, his beans may be infested with maggots from eggs deposited at that time.

In 1919 an attempt was made to connect the time of fly emergence and the time of oviposition with some of the more obvious occurrences in

nature. In that year, and also in 1920, the first flies were taken in small numbers early in May, about the time when cherries were in bloom. Mature flies were out in numbers near plowed ground on June 2, 1919, at which time the last of the petals had fallen from late apple trees at Perry. Flies with fully developed eggs had not been found in quantities on plowed ground before this, altho a few females with immature eggs had been collected in winter-wheat and oat fields. Many eggs were deposited in cages about June 4. Dissected females showed that some eggs were mature on June 2 and many on June 4. It is evident, therefore, that under Perry conditions in 1919, beans planted between June 2 and 12, or within ten days after the last of the petals had fallen from the late apple trees, were open to maggot attack. Serious infestations of maggots were very few in 1919, but in two bean fields which did show *cilicrura* injury the seed was planted on June 5 and June 6, respectively.

On May 28, 1920, when the petals had partly fallen from the late apple trees, flies nearly mature were found in numbers on moist, newly turned ground, especially where the field had previously been in sod. After May 7, when the first specimens of the year were taken, adult females were captured almost daily and their abdomens examined for eggs. Between May 7 and May 28, a few flies with ripe eggs were occasionally found, showing that eggs were doubtless deposited in small numbers during that period. A cornfield planted on May 22 and examined on May 29 showed typical *cilicrura* injury in a few seeds. However, this examination of females taken thruout May showed that most of the first brood of flies were not mature before May 28. At that time there were many more females than males present on plowed ground. Many eggs were deposited between May 28 and June 7 by flies in the cages. Most of these eggs were deposited after June 1, when the nights as well as the days were warm and the flies showed unusual activity.

Many fields in which beans were just appearing above ground were examined on June 7, 1920, and only six infested plants were found. Good weather had made it possible to plant some of these beans by May 21, and all were in before June 1. Therefore, in these fields, the seed was in the ground before most of the flies were mature, with the result that there were but few maggots in the soil.

Beans planted in the experimental field on June 4, 1920, were heavily infested, and potatoes and corn planted in neighboring fields about the same time contained many maggots. This infestation is probably due to the fact that the seed was put into the ground at the time when the flies were mature and eggs were being deposited. Beans planted in the middle of June were uninjured. From these data it would seem that beans planted just after the last apple blossoms have fallen, which under the conditions at Perry in 1919 and 1920 was from May 28 to June 7, stand a greater chance of being infested by the maggots of *H. cilicrura* than do those planted

before or after these dates. Since the larvae already in the soil may attack the newly planted seed, it is wise to delay planting for a few days after all the eggs have been deposited. This would extend the time for probable infestation in 1919 and 1920 from May 28 to about June 15. Unfortunately, it is not always possible to choose the time of planting as suggested above. Weather conditions may prevent planting in May, before the flies are mature, and if beans are put in too late in June they may not ripen before they are killed by frost. Seasons vary so much from year to year that no absolute rule can be given; but, if weather permits, it is best to plant before the oviposition period of the flies, when the last of the petals have fallen from late apple trees.

Relation of kind and condition of soil to maggot infestation

Abundant moisture provides favorable conditions for the development of *Hylemyia cilicrura*, as is shown on page 970. Beans on heavy soil, which holds moisture, grow more slowly, decay, and furnish conditions attractive to the flies for oviposition. In 1917 one side of a bean field near Perry was badly infested, while the remainder, which was planted on the same day, was free from injury. An examination of the soil in the infested part showed it to be heavy and sticky, while the unattacked beans were growing in lighter soil of a sandy constituency, which was relatively dry. The division between the two types of soil was very marked, and the good and the poor beans followed this line closely. Well-drained fields are not attacked as often as are those where the drainage is poor. Low and wet spots, where water may collect in otherwise good fields, often yield poor beans. This is in part the result of maggot work, but it may often be due to the decay caused by the excess of moisture in the soil.

Warm, dry soil that is well fitted furnishes ideal conditions for the growth of beans. In soil of this kind they will germinate quickly, and when once above ground there is little chance of serious injury from maggots. In wet seasons it is best to delay planting until the soil can be well fitted. A field should be dragged and rolled, and the top layer of earth allowed to dry out and become warmed by the sun.

Influence of preceding crop and time of fitting a field, on maggot attack

Heavy infestations of *Hylemyia cilicrura* have been found on land that had previously been in potatoes, corn, tomatoes, wheat, oats, and beans, as well as in clover and alfalfa sod. Many infestations have followed sod, since the upturned roots of decaying clover and alfalfa furnish good breeding conditions for maggots, and since clover forms a part of a regular rotation of beans, wheat, and clover which is practiced in western New York. Just as serious outbreaks have been found, however, where the preceding crop was beans, especially if the field had an abundance of quack grass and weeds. In the writer's garden there was a patch of quack grass. This was turned under, and beans and peas planted on

this spot were infested with maggots, tho in other parts of the garden there was no injury.

Whelan (1916) has found maggots in fresh manure, and he says:

> Furthermore, it appears that while beans were apt to suffer when planted on freshly turned clover sod, especially if recently fertilized with undecomposed manure, they stood a much better chance of escape if the field was prepared early in the season and the maggots given a chance to develop and disappear before the beans were planted.

Tho the writer has been unable to find evidence of flies breeding in manure, he has found many maggot-infested fields which had been covered with manure just before plowing. It must be said, however, that serious outbreaks have been found where manure was not used.

If a field is fitted early and is allowed to dry out before the mature flies seek places to oviposit, it appears to be less attractive for oviposition than newly turned soil. In 1920 the laboratory field was plowed at a time when flies with well-developed eggs were numerous, and many bean seedlings were infested. Fields near by that were plowed earlier and allowed to stand were free from maggots.

Relation of depth of planting to injury by maggots

Beans planted deep in the ground take longer to reach the surface and are thus exposed for a longer period of time to maggot attack. It has been observed many times that beans planted deep in wet ground suffer more from *Hylemyia cilicrura* than those that are planted less deep. For example, in 1917 it was often noticed that the headlands yielded better beans than the remainder of a field. This is attributed to the more shallow planting, for the soil was not so loose at the edges of the field and therefore the drill did not sink so deep.

In 1917 a field under observation had nearly every bean attacked by maggots. The seed had been planted in wet soil at a depth of from three to five inches. After this first planting was destroyed by maggots, the field was reseeded at once, and the beans were dropped as near the surface of the ground as possible. Some of the seed was even left on top of the soil, and a boy with a hoe followed the machine to cover the beans left exposed. A 95-per-cent stand resulted.

In another case a grower started to make a very shallow planting of beans. When he had gone part of the way across the field, he decided that he was not getting the seed in deep enough, and so he planted the remainder of the seed much deeper. At harvest time the beans planted first, the shallow-planted ones, were the only ones worth harvesting. If the beans are planted too deep, many will decay because of the excessive moisture, and the maggots will destroy a large proportion of the remainder

Experiments were conducted in 1917 to test the effect of the depth of planting on the time required for the beans to break thru the soil. Beans were planted on good, tho very wet, soil on July 12. When the field was

examined on July 19, the beans that were planted about one inch deep were nearly all up, those planted three inches deep were about half thru the soil, and none of those planted five inches deep were yet above ground. In another wet field 100 seeds were planted at depths of one, three, and five inches, on July 16. On July 23 there were, in the one-inch planting, 57 plants, of which 4 were snakeheads; in the three-inch planting there were 35 plants, of which 5 were snakeheads; and none of the beans planted five inches deep had appeared above ground. In the laboratory field, under rather warm, dry conditions in July, 1918, it was found that beans planted three inches deep came up nearly as quickly as those planted more shallow.

Summary of preventive measures

The results of experiments on artificial control measures, such as coating the seed before planting and treating the soil with materials of a repellent nature, afford small hope for their future successful development. As a result of a study of some of the factors governing infestations, the possible preventive measures that have been discussed in the foregoing pages are summarized in the following paragraphs.

The seed-corn maggot is more serious as a pest when the months of May and June are rainy, and the ground is cold and wet at bean-planting time, than under other conditions. The greatest injury results when several unfavorable years occur in succession. *Hylemyia cilicrura* thrives when oviposition takes place under wet conditions; and therefore it is wise to plant when the soil is dry and the earth is warm. The soil should first be well fitted with a disk or a harrow, and then rolled, and finally, after a few warm days have dried out the top soil, the beans should be planted. If the field is fertilized in order to hasten the germination of the seed, there is a still better chance of getting a stand. However, fields fertilized with fresh manure just before plowing often show a heavy infestation of maggots, and so this condition should be guarded against in wet years.

As maggots developing from eggs deposited on newly tilled ground are often found in decaying matter in the soil, it is sometimes wise to fit a field early, before most of the flies are sexually mature. The ground will then be dried and less attractive to flies for oviposition by the time they come out. The presence of many flies of this species crawling over newly turned soil between plowing and planting time is a good indication that seed planted there will probably be infested. In 1918, 1919, and 1920, sexually mature flies were most numerous in the fields at Perry from May 25 to June 10. In 1919 the greatest number were present about June 4, and in 1920 about June 2. If the weather permits, it is better to plant ahead of this brood. If this is impossible, planting should be delayed until the flies are less common.

It is extremely important that beans should not be planted too deep in wet soil. If they are, some of the seed will rot and the maggots will destroy

most of the remainder. Not only is the soil three or four inches below the surface much colder and more moist than the top inch, but also the deeply planted seed germinates more slowly in wet years. It is wise to force seed to germinate and grow as rapidly as possible, since it will have escaped serious injury when it is once above ground. If in shallow planting some of the beans are left on top of the ground, they may easily be covered with a hoe. A bean planter or a corn planter usually will give better service than a drill in wet years, for either is lighter and will not sink so deep in wet places. If a drill is used, it should be adjusted to make a shallow planting. A grower who plants his seed deep in wet soil at a time when the sexually mature flies are numerous, is sure to have a heavy infestation of maggots on his beans.

THE IMPORTED FIELD GRAY SLUG
(*Agriolimax agrestis* L.)

ORIGIN

The field gray slug, or garden slug (*Agriolimax agrestis*, Plate LXIX, 6), is an imported species which, with two other foreign forms (*Limax maximus* L. and *L. flavus* L.), does more damage and attracts more attention than all of the other twenty-nine species of slugs reported from the United States (White, 1918). *A. agrestis* is an old res dent of Europe, having been listed in England as early as 1674. Taylor (1907) reports it in the fossil rocks of the Pliocene and Pleistocene periods from many places in the British Isles, as well as from Germany and France. It apparently came to this continent from Europe early in the eighteenth century.

HISTORY AND DISTRIBUTION

Theobald (1905) states that *Agriolimax agrestis* is found in near'y every garden in England, and also on the continent of Europe and in Siberia, Madeira, and Algeria. Taylor (1907) states that it occurs also in Turkestan, China, Japan, Asia Minor, Morocco, Cape Colony, Zanzibar, Australia, and New Zealand, as well as in Brazil, Jamaica, and parts of Canada, on this continent.

In the United States it was first reported near the seaports of Boston, New York, and Philadelphia. De Kay (1843) states that Binney knew it before 1843, tho Binney (1851) still had trouble in separating *A. agrestis* from the native species *A. campestris*, which it very much resembles. Since 1851 *A. agrestis* has spread gradually westward, and it is now found locally in many States. Its presence is reported in the literature of Maine, Massachusetts, New York, Pennsylvania, Michigan, New Jersey, Illinois, Wisconsin, Ohio, Colorado, Washington, and California, but it is probably present also in many other parts of the country. Slingerland discovered the slug at work on the college farm at Ithaca in 1891. Baker

(1902) did not find it around Chicago in 1902, tho it had been reported from Michigan in 1899. Cockerell[6] found *agrestis* in Colorado in 1890, and he states that it was brought there from New Jersey. He reports it also in Oregon in 1891 and in California in 1892.

In western New York the localities infested by *A. agrestis* are increasing, and in wet seasons many beans, as well as other field and garden crops, are injured. The insect is apparently not a pest in all sections of the bean-growing counties, but appears to be limited to a few farms and gardens in each district. Some places seem to be entirely free from it. It is often abundant on small truck farms, and around the shrubbery and the gardens n city lots. It has, no doubt, been carried into its present habitats in the straw or moss packing of bulbs, shrubs, or nursery stock. Disseminated in this way, it seems to thrive, and it apparently prefers cultivated crops to woods and pasture land. As it becomes better established the species may be expected to spread from the present centers of infestation until it is of almost general distribution. The long, cold winters often experienced in New York, however, should tend to prevent the serious damage that it causes nearly every year where the climatic conditions are milder and more uniformly moist.

SYSTEMATIC POSITION

The field gray slug belongs to the phylum Mollusca and the class Gastropoda, which includes the slugs and the snails. *Agriolimax agrestis* is placed in the family Limacidae, the members of which have no external shell. This family, according to Pratt (1916), is represented in America by only six species. The large spotted slugs of the family are now placed in the genus Limax L., while smaller forms, such as *agrestis*, belong in Agriolimax Morch. Because of its varied coloration, this slug has been described under many specific names. Taylor (1907) gives a complete synonymy for the species, and lists ten varieties, with the localities from which each has been reported.

GENERAL DESCRIPTION OF THE SLUGS OF THE FAMILY LIMACIDAE

The field gray slug belongs to the same group of Mollusca as the snails, and differs from them but little except in the size and form of the shell. In slugs of the family Limacidae no shell is visible on the outside of the body, but there is a thin calcareous plate (Plate LXIX, 5) concealed in the mantle — the fleshy shield over the front part of the slug. The body is elongate-subcylindrical, and bears a more or less prominent dorsal keel. On the retractile head are two pairs of tentacles; the anterior pair aids in feeding, while the upper, or posterior, pair bears the eyes. The eyes have the form of rounded knobs on filament-like stalks. When the slug is disturbed,

[6] As cited by Taylor (1907:120).

the eyes may be withdrawn down the tentacle, and in young, transparent specimens they may be readily seen even after they have been retracted into the head. Slugs have the power of secreting from pores in the body, and especially from the anterior ventral surface of the foot, a slimy substance known as *mucus*. The shell-concealing mantle has, near its posterior lower border on the right side, a circular breathing pore which opens into a respiratory chamber beneath. This is lined with a richly vascular epithelium subserving the function of a respiratory organ. Just behind the right eye-stalk is the opening of the genital organs, thru which eggs are extruded. Slugs of this group are hermaphroditic, both male and female genital organs being present in a single individual.

ANCIENT SUPERSTITIONS CONCERNING SLUGS

Slugs have been known in Europe for many years, and the older writings in regard to them contain many interesting notes. They have been used as food in Europe, and it is said that as late as 1863 they were prescribed by French physicians, to be taken in the form of a sirup. A slug distillate was considered good for the complexion (Kingsley, 1885). A plaster of slugs with the heads removed, bound on the forehead, was believed to cure a headache, and slugs eaten alive in milk were thought to cure consumption (Rogers, 1908).

As slugs always appear after a rain, they were believed by English farmers in the eighteenth century to come from heaven in a rain cloud (Theobald, 1895). Since toads gather in infested fields to feed on the slugs, it used to happen that gardeners and farmers of a hundred years ago, finding that their plants had been destroyed during the night, would blame and kill the toads, while the real culprit was concealed in a safe retreat under ground (Ritzema Bos, 1890). Later, the value of toads as enemies of the slugs was appreciated and three francs a dozen was paid for them (Guénaux, 1904). Years ago the small shell of the slugs was regarded as an amulet, which, worn on a string around the neck, was believed to protect the wearer from harm. When the slugs suddenly appeared in large numbers in the gardens of European countries, it was customary to invoke the power of the Church against them, in the hope that they might be thus removed (Kingsley, 1885); and Taylor (1907) states that the Ritual of Paris, A. D. 1712, contains definite exorcisms for this purpose.

PECULIAR HABITS OF SLUGS

Some slugs are said to have a partiality for moist newspaper, dead fish, earthworms, dead clams, dead slugs, meal, flour, cream, butter, Pears' soap, sponge cake, and book bindings, as food (Cooke, 1895). They have been known to eat out the corks of wine bottles, to crawl into nearly empty beer bottles and bathe themselves in the contents, and even to attach their small mouths to the dripping faucets of containers of

alcoholic beverages. They will crawl into beehives and feed on the honey, apparently immune to the stings of their enraged hosts (Reh, 1913).

ECONOMIC IMPORTANCE

In wet years the field gray slug is one of the two most destructive animal pests of field beans in New York. During the rainy summers of 1916 and 1917, nearly all of the plants in some fields were attacked and many were entirely destroyed. Estimates of the losses on twenty-one farms in Orleans County in 1917 varied between 5 and 70 per cent. In 1918 the writer saw a bean field in Monroe County in which about one-third of a ten-acre field was so badly attacked that not a trace of a plant was left above ground.

In addition to its attacks on field beans, the slug often causes much injury to garden beans, lettuce, cabbage, peas, potatoes, radishes, and strawberries. As the species becomes better established in the farms and gardens in new localities thruout New York, it is probable that more widespread attacks may be expected on crops during wet seasons.

NATURE OF THE INJURY TO BEANS

Immature specimens of *Agriolimax agrestis* eat the tender tissue between the veins and the veinlets of the leaves, thus giving them a skeletonized

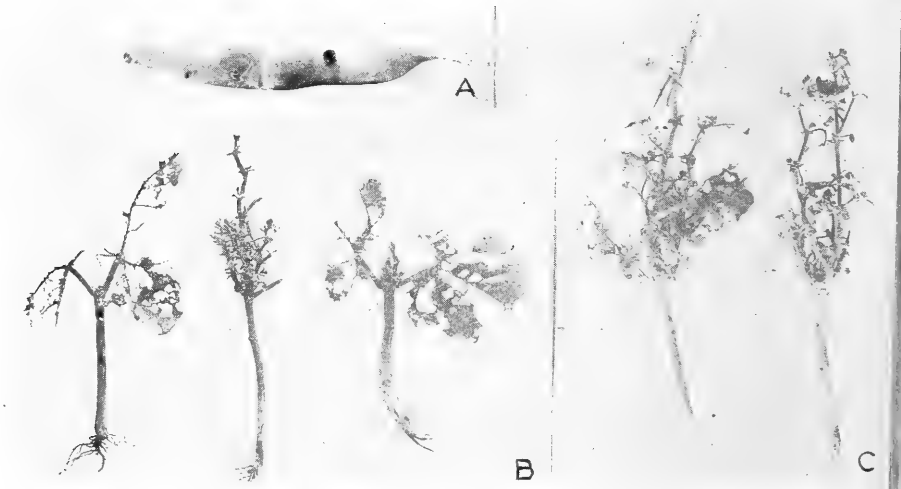

FIG. 91. INJURIES CAUSED BY AGRIOLIMAX AGRESTIS

A, A bean pod showing a hole made by the slug in feeding. B, Bean plants injured by slugs. (Photographed in midsummer.) C, Bean plants that were injured by slugs soon after they appeared above ground, photographed at harvest time.

appearance. Older slugs, however, eat parts from the edges of the leaves, and frequently continue to feed until every leaf is devoured (fig. 91, B).

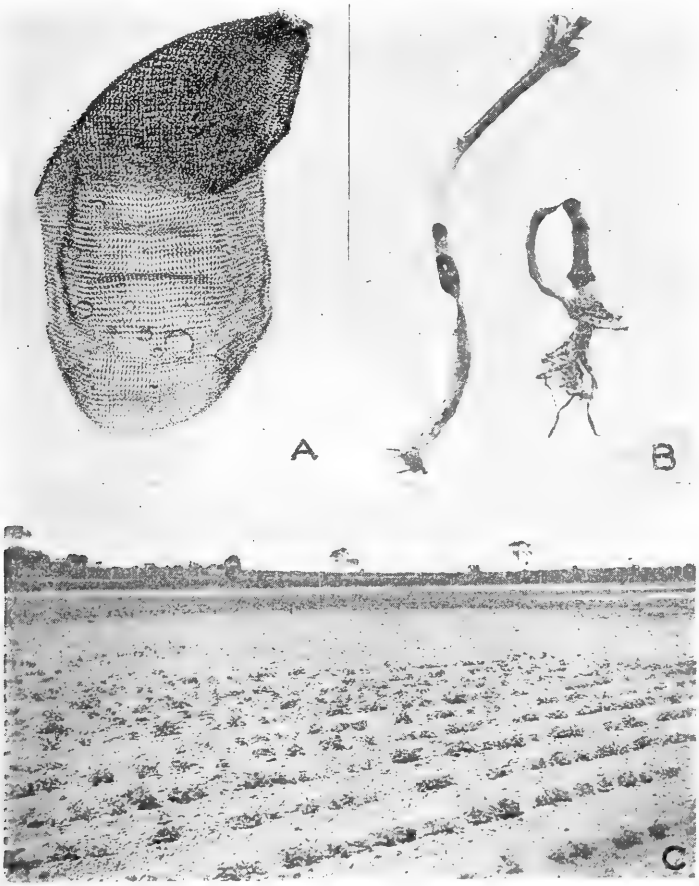

FIG. 92. RADULA OF AGRIOLIMAX AGRESTIS, AND RESULTS OF WORK OF SLUG

A, Radula, or lingual ribbon, of slug, made up of many hundred small, sharp teeth, × 25. B, Young bean plants showing result of feeding by the slug. C, A bean field in Monroe County, New York, in parts of which all the plants were destroyed by slugs; bare areas shown.

Sometimes the petiole and a few of the main veins are left, but oftener the entire plant above the surface of the ground is destroyed. During

the daytime and in dry weather the slugs feed beneath the ground, eating large parts of the stems of plants (Plate LXX, 2, and fig. 92, B). Such plants may be so severely injured that a wilting of the parts above ground results.

When a slug crawls up the stem of a young bean plant, it usually devours the budlike growing tip before it moves on to the leaves. Plants of this kind are always stunted and show an abnormal, useless growth of small leaves (fig. 91, C). Such plants commonly die, and even when they survive they fail to produce mature seeds.

If the slugs are numerous at the time of pod formation, it is not unusual for them to eat holes into the sides of the pods (fig. 91, A) and feed on the soft beans within. Often several holes of this kind are found in a single pod, and sometimes a slug after destroying one bean will move along inside the pod and feed in turn on all the remaining seeds.

INJURY TO PLANTS OTHER THAN BEANS

In its nocturnal feedings above ground, *Agriolimax agrestis* seeks the tender leaves of lettuce, corn, cabbage, and cauliflower. The injury which the slug does to these plants is similar to that which it produces on large bean leaves, and causes the plants to become unhealthy and unmarketable. When the weather is such that the slugs are active in late summer, they frequently eat large holes in the sides of ripe tomatoes and fall strawberries, in addition to eating the leaves.

The pest feeds underground on potatoes, and, together with the millepede *Julus caeruleocinctus* Wood, causes considerable damage in western New York by eating out large cavities in the tubers. Carrots, turnips, radishes, and beets suffer similar attacks on their fleshy roots.

HOSTS AND POSSIBLE FOOD SUPPLIES

Agriolimax agrestis has such a wide range of food plants that it is classed as almost omnivorous. Among the plants which it feeds upon are cabbage, potatoes, eggplant, lettuce, beans, lima beans, peas, corn, strawberries, gooseberries, cucumbers, melons, cauliflower, wheat, turnips, beets, carrots, radishes, celery, clover, oats, dahlia, dandelion, dock, chicory, tobacco, hops, and tomatoes. There are also many weed hosts on which this mollusk may be found, such as burdock, ragweed, lamb's-quarters, and mustard. It finds palatable several species of mushrooms also, and many ornamental shrubs and vines, and it finds abundant food in sod land and in lawns. Overgrown places in fence corners and along the edges of fields often harbor many of the slugs. Manure is acceptable to them as food, and their eggs, as well as young slugs, have been observed in large numbers where manure had been scattered in piles around a field. Cooke (1895) mentions as among the possible foods of *agrestis*, may-flies, beetles, and dead

slugs; Lovett and Black (1920) add sow bugs, earthworms, and aphids to this list; Taylor (1907) records a case in which *A. agrestis* killed and ate slugs of the species *A. campestris* when the two were placed in the same box; and Lebour (1914–15) finds that they eagerly devour the proglottides of Moniezia, a tapeworm of sheep. It would seem, therefore, that, while the slugs usually prefer a vegetable diet, under some conditions they relish animal food.

DESCRIPTION OF STAGES

The egg

The egg of *Agriolimax agrestis* (fig. 87, C, page 954) is elliptical or spherical in shape, and is translucent, jelly-like, bluish white, and iridescent. Under magnification the thin outer covering is found to be slightly roughened with regular raised and depressed areas. The eggs are found either singly or in masses, in the latter case being held together by a transparent secretion. On one end the small, projecting micropyle is visible, especially in newly deposited eggs. The eggs vary from 1.6 to 3 millimeters (1/16 to 1/8 inch) in length.

The young slug

A newly hatched specimen of *Agriolimax agrestis* is without definite form at first, but it soon assumes much the same appearance as its parent except that its tentacles are relatively larger and its body is transparent, permitting the black nerve cord running to the eye to be easily seen thru the body covering. Young slugs have a pinkish tint at first, but later turn to darker hues as they begin feeding.

The full-grown slug

The slug (Plate LXIX, 6, and fig. 87, D) is described by Taylor (1907:105) as follows:

> Animal limaciform, with large but flattened tubercles; of a somewhat uniform whitish or pale ochreous ground colour, but sometimes dull lavender or other tint, often mottled, speckled or reticulated with brown or black, and at times totally suffused with black; body somewhat compressed and keeled towards the tail; tentacles dark coloured; shield more than one-third the total length of the animal, rounded in front and behind, concentric striae not deep, with the nucleus on the right side and towards the rear; respiratory orifice with a broad usually unpigmented raised ring, which is cut anteriorly by the anal cleft; sole pale and longitudinally tripartite, the side areas sometimes darker, especially towards the tail; sole-fringe separated as usual from the body by a furrow, containing a row of elongate tubercles, upon which the body tubercles rest unconformably. Mucus plentiful and viscous, often clear when crawling, but becoming milky-white on irritation, due to innumerable particles of carbonate of lime.
>
> Length usually about 35 mill.

LIFE HISTORY AND HABITS

The egg

Under New York conditions, some of the eggs of *Agriolimax agrestis* are deposited in the fall, from August until December, and many of the mature slugs die soon afterward from the cold. If full-grown slugs live thru the winter, they may deposit eggs during May and June of the following spring. Slugs developing from these overwintering and spring eggs will mature and in turn deposit eggs in the fall of that year or in the following spring.

In the summer of 1917, which was very wet, eggs were deposited more or less continuously from May to December, being especially numerous in September and October. Theobald (1905) reports this to be the normal condition in England. Lovett and Black (1920) state that in Oregon egg-laying occurs at all seasons of the year, and that the greatest number of eggs are deposited in the spring and early summer.

In 1918, which was a drier and more nearly normal season for New York than the preceding years had been, eggs were deposited by the slugs in cages during May and June, and not again until September 23. In that year, as well as in 1919, most of the eggs were deposited late in October and during November. Moisture is a factor of great influence. A few of the eggs deposited in July and August of 1917 hatched that fall, but whether these young slugs survived the cold winter that followed is not known.

The dates of hatching for eggs deposited on May 4, 1918, by an overwintering slug were as follows: May 27, three; May 29, two; June 1, four; and June 2, five. The average length of the egg stage was 26.5 days. Eggs that had been deposited late in the previous fall hatched between May 10 and June 6, the length of the egg stage in this case being between six and seven months. Early in the summer all the slugs in the fields are about the same size, and it is therefore probable that the fact that some eggs are deposited in the spring and others in the fall has little influence on the hatching date

During the winter of 1917–18, there was in the greenhouse, where the temperature ranged from 55° to 75° F., a wide variation in the length of the egg stage, which ranged from 26 to 57 days, the average for 189 eggs being 37.3 days. In a greenhouse which was kept at a constant temperature of 80° F., 24 eggs hatched in an average of 24.3 days. Theobald (1905) gives from three to four weeks as the normal egg stage in England.

The eggs of *A. agrestis* are tucked into crevices of the soil, not far below the surface of the ground, and are also hidden under rubbish and projecting stones, around the walls of buildings, and among the roots of grass. In bean fields that have been badly infested, the slugs collect under the bean piles in the fall and deposit many eggs. In the fall of 1917 more than five hundred slugs were taken under a pile of this kind, and the eggs were

countless. Slugs thrive in sod land and many eggs may be found in the spring around the roots of grass in fence corners and in meadows.

One pair of field gray slugs may deposit from 500 to 800 eggs, according to Theobald (1905). This writer says that the eggs are given out in batches of about 50 at a time, cemented together in piles of from 6 to 15. Taylor (1907) cites a case in which a pair of *agrestis* deposited 774 eggs during the season, and Lovett and Black (1920) found 612 eggs deposited by one specimen between May and the following April. One slug, found by the writer early in the spring, deposited 180 eggs between May 5 and June 19. Two slugs confined in one cage have produced as many as 464 eggs before they died, and it is probable that, due to cage conditions, this was less than the normal number.

Many eggs of *A. agrestis* do not hatch. After the severe winter of 1917, the writer was unable to find a single egg in the spring where there had been thousands in the fall preceding. This natural destruction is, without doubt, a great help in reducing the numbers of the pest in western New York. While the eggs need moisture for their development, excessively wet surroundings are unfavorable, for under such conditions they become moldy and spoil tho they may retain their normal shape. In a dry environment, the egg covering will shrivel and the egg will contract until it might be mistaken for a particle of the dirt on which it rests. When moisture is added, however, it will again swell to normal size. Bland and Binney (1873) describe experiments in which eggs of *A. agrestis* were dried many times in a desiccator, in some cases being kept in this condition for several years; when these eggs were again placed in normal moist surroundings, they assumed their usual shape and hatched. Since the development of the embryo in the egg is easily observed, much study has been given to this part of the life cycle by Mark (1881), Kofoid (1895), and Byrnes (1899).

The young slug

Newly hatched specimens of *Agriolimax agrestis* differ but little in their habits from the full-grown slugs. Because of the limited food supply in proportion to the large number of slugs hatching from a single egg mass, these slugs appear gregarious. As they become older and more hardy, they migrate from the original center and spread out in search of other food. Cooke (1895) reports that on hatching they go into the ground for four or five days before feeding. The writer had noted that green food in cages did not show strong evidence of feeding for several days after the slugs hatched, but he had attributed this to the small size of the radula, or rasping organ, at this time.

The young slug often secretes its slime in such large quantities that it is able to descend from plants to the ground on a thread of this material. Taylor (1907) states that this slime thread is the same as the trail left by the slug wherever it crawls, except that it is freed from contact with the

earth. The same writer declares that *agrestis* is able to descend at the rate of five inches a minute on a thread of this kind, and that one specimen was found hanging on a thread seven feet from the point of attachment. At times they reascend by this same thread.

The full-grown slug

The adults of *Agriolimax agrestis*, as well as the young, are nocturnal. They are seen during the day only in cloudy or rainy weather, or in shady and concealed places. In an infestation under observation on July 13, 1918, the slugs were on the plants from seven o'clock in the evening until eight in the morning. As it becomes light, the slug crawls into a crevice of the soil or under some protective covering such as grass, straw, or boards. This aversion to light is said to continue even after the eye-bearing tentacles have been removed. In a bean field the slugs frequently burrow down near a bean plant and feed on the parts below ground. The writer has found them buried from four to eight inches deep in the soil, with their tentacles drawn in. They were contracted and inactive, and were covered with a coating of slime to which particles of dirt adhered. In the cold weather of winter they hibernate in this resting position.

The field gray slug moves by an almost imperceptible shortening and lengthening of the muscles of the foot, or under side of the body. Taylor (1907) declares that two inches a minute is a good speed for this species, and has estimated that at this rate it would take twenty-two days and ten hours of steady movement to cover a mile. Since the slugs have been in this country they have apparently absorbed some of the American spirit, for they have been observed to go much faster than this. Some slugs are reported to return to the same hiding place night after night, but *agrestis* apparently does not have this habit.

The nocturnal travels of the slug are recorded each morning by the trail of slime which the animal leaves wherever it goes. After a rain these slime trails are often found on sidewalks, and in heavily infested fields the writer has seen the ground and the plants so coated with this glistening secretion that they have an iridescent appearance. More slime is secreted on a dry surface than on one that is moist, and on the dry surface the slime appears more milky, due, it is believed, to the presence of particles of carbonate of lime. This mucous secretion is supposed by some writers to aid in locomotion, while other writers declare that it regulates the evaporation, thus controlling the body temperature. It is thought also to serve as a protection against enemies. When irritated by a finely pulverized substance, such as lime, *agrestis* will give off large amounts of slime from the pores of its body, and when this mixes with the powder it usually forms a coat around the animal. The slug is sometimes able to escape by leaving this coat behind, but it may become so weakened by its struggles that it dies within the covering.

Method of feeding

Agriolimax agrestis does not eat in the same manner as does a biting insect, for its feeding apparatus is very different. The jaw (Plate LXIX, 10) is a concave, chitinous process attached to the roof of the pharynx. In the center it bears a tooth with finely serrate edges, which helps in tearing food apart. Opposed to this, on the floor of the pharynx, is a flexible plate made up of many small, sharp teeth, known as the radula (Plate LXX, 1, and fig. 92, A, page 981). This radula, or lingual ribbon as it is sometimes called, is supported on the muscular tongue and may be moved forward and backward. By the combined use of jaw and radula, small particles of food are torn from a plant and are then passed on to the stomach. Cooke (1895) states that the teeth of the radula are sharp enough to break the skin of the human hand if the slug is permitted to use this organ for a short time in one place.

Mating and oviposition

It has been previously noted that *Agriolimax agrestis* is hermaphroditic, both male and female sexual organs being found in the same individual. Whether or not the slugs are capable of self-fertilization is not definitely known. Theobald (1905) says that self-fertilization is rare, and that the male and female reproductive organs mature at different times. In the winter of 1917–18 the writer isolated specimens of *agrestis* a few days old and kept them in breeding jars in the insectary. One slug, on reaching maturity, deposited a few eggs; but because of an accident to the heating plant at a time when the temperature was far below zero, these eggs were frozen. Since that time it has been impossible to obtain eggs from isolated specimens, and therefore it cannot be said whether eggs of this type are fertile.

On the evening of July 7, 1920, the writer saw for the first time the sexual union of *A. agrestis*. Two specimens, one much larger than the other, were crawling around and around each other on a patch of slime about an inch in diameter. Sometimes they would strike each other with their tentacles. Soon the excitatory organ, or sarcobelum, was extruded, and this also was used in a caressing manner. After this behavior had continued for about three-quarters of an hour, the sarcobelum of each slug enlarged very greatly; the two organs came together and there was a great discharge of slime. In regard to the actual transfer, Taylor (1907:107) says, "The seminal element, mixed with mucus and worked up into a little ball, is transferred bodily, the forerunner of a true spermatophore."

Time required to reach maturity

In ordinary years, under field conditions in New York, slugs that have developed from eggs hatching in May are ready for oviposition in October

of the same year. This makes the time to sexual maturity about five months. In the wet season of 1917 this period was shortened to three months for some individuals. When the slug overwinters, it may be more than twelve months before it begins to deposit eggs.

Many specimens of *Agriolimax agrestis* that hatch in the spring do not live thru the following winter under New York conditions. In no case have slugs under observation lived thru two winters. This would make the greatest length of life actually observed in New York about eighteen to twenty months.

In European writings it is stated that *A. agrestis* may live for several years (Theobald, 1895); also, that the slugs are sexually mature in six weeks, and that there may be several generations in a year (Reh, 1913). Cooke (1895) reports that slugs of this species are usually full-grown by the middle of the second year and die during the first part of the third year. Taylor (1907) cites one instance in which a slug mated and deposited eggs in sixty-six days, was full-grown in eighty-two days, and lived for about eighteen months. The same writer states that the time from hatching to maturity probably varies from ninety days to nearly one year.

NATURE OF OUTBREAKS

When the outbreaks of *Agriolimax agrestis* occurred in 1917, it was noted that ordinarily the bean fields were evenly attacked. All the plants showed some injury to leaves and vines, but only a few were completely destroyed. The exception to this was in a field where a large tree, with its border of sod, seemed to act as a center from which the slugs migrated. In the grass near this tree were found many eggs and adults of *A. agrestis*, showing the place to be the local seat of infestation.

Only one outbreak of *agrestis* was observed by the writer in New York in 1918, and that was in Monroe County, in a slightly rolling field where the knolls had been covered with horse manure in the preceding fall. This field had been in sod for several years. The infestations seemed to start from the knolls, and when the field was seen by the writer the plants had been entirely destroyed as far as the slugs had migrated (fig. 92, C, page 981). Leaves and vines were completely devoured and the parts below ground were also attacked. The infested area grew larger each night as the slugs moved forward along the rows. In this infestation slugs of all sizes were present; the larger ones (40 millimeters) were in the front ranks of the advancing hosts, while far back in the devastated part of the field were the small ones (4 millimeters), which had been left behind in the rapid advance. This variation in size is unusual in New York and was probably the result of the exceptionally good hibernating place provided by the manure and sod of the field, which no doubt had allowed more or less continuous development thruout the winter.

RELATION OF AGRIOLIMAX AGRESTIS TO MOISTURE

Agriolimax agrestis is a moisture-loving animal. It is found above ground in large numbers only after rains or on cloudy days when the relative humidity is high. In 1916 and 1917, wh ch were damp years at Perry, the slugs of this species were unusually active in the bean fields. During the past three years there have been no extensive, general outbreaks. From an examination of the relation of the rainfall of the past four years to the abundance of the slugs, it would seem that rainy weather in May and June, when the eggs are hatching and the young slugs are beg nning their growth, makes conditions most favorable for their development. Especially is this true if two or more such years come in succession. In 1916, and again in 1917, these months were rainy. In June of 1916 the rainfall at Rochester, New York, was 5.72 inches, and for the same month in 1917 it was 6.40 inches; while in 1918, 1919, and 1920, it was below the monthly average of 3.13 inches.

It sometimes happens, after a rainy period, that the ground dries and bakes so hard that the slugs cannot break the hard crust and are thus forced to feed below the surface. On heavy, undrained soils the damage is always greater than on lighter ground. Since the growth of the slugs is dependent on the amount of food eaten, and since their feeding is heavier in moist surroundings, it is easy to see why they mature much more quickly in moist than in dry seasons. During dry periods the slugs are found deep in the soil, in contracted positions. They work their way far below the surface of the soil in search of moisture. Reh (1913) says that a slug supplied with plenty of moisture after having been under dry conditions, may become three times as large as it was before.

RELATION OF AGRIOLIMAX AGRESTIS TO EXTREMES OF TEMPERATURE

The field gray slug can survive cold weather if it is in a protected position; but a temperature of −14° F. proved fatal to specimens in flower-pot cages in the insectary at Ithaca when there was no fire in the building for several days. Few slugs survived the unusually cold winter of 1917–18, as was shown by the fact that in the spring of 1918 the writer could find but a small number in the fields near Perry where there had been thousands in the fall preceding. The slugs that had escaped the cold had done so by crawling under the sod and the rubbish in fence corners or other protected places. Very few of the millions of eggs deposited under the bean piles in the fall of 1917 survived. These occasional severe winters are believed to have an important influence in keeping down the numbers of this pest in New York. January of 1918 was the coldest January, as well as the coldest month, within the scope of the official weather records. The mean monthly temperature for that month at Ithaca was 9.7 degrees

(Fahrenheit) below the normal. The first half of February was also unusually cold. Since that year slugs have been so scarce that injury to beans caused by them has been almost unheard of.

In the study of the distribution of *Agriolimax agrestis*, it may be noted that it has not been reported as serious in the Southern and Middle Western States. This is perhaps because the high, dry temperatures of these States during the summer are unfavorable to its successful development.

SEASONAL HISTORY

In western New York there is normally but one generation of *Agriolimax agrestis* in a year. Sometimes the eggs deposited in the fall hatch in the following spring, and the slugs from these eggs are full-grown by August and, in their turn, deposit eggs from September to December. These adult slugs usually die before the next spring. Sometimes, however, full-grown slugs live thru the winter and deposit their eggs in May and June of the next year. These spring eggs hatch at about the same time as the overwintering eggs.

PREDATORY AND PARASITIC ENEMIES

In England, acording to Theobald (1905), slugs are preyed upon by the thrush, the starling, the pigeon, the blackbird, the duck, and poultry, as well as by the toad, the shrew, the mole, and the centipede. Ritzema Bos (1890) states that in France, beetles of the families Carabidae, Staphylinidae, and Lampyridae feed on slugs; and Cooke (1895) reports that there is a fly which lays its eggs with those of *Agriolimax agrestis*, and that the slug is parasitized by the larva. The same writer says also that nematodes likewise help to reduce the numbers of these slugs. Banks (1915) reports that a mite (*Ereynetes limaceum* Koch) has been found attached to some species of slugs.

In western New York, chickens free to run in the fields have eaten many slugs. Eggs of the species in a wet petri dish were found to have nematodes feeding in them. The small worms would apparently make a hole thru the outer covering of the egg and feed on the embryo within.

CONTROL

Various control measures against *Agriolimax agrestis* have been tried and recommended. In many cases advantage has been taken of the irritation and the secretion of mucus caused by finely pulverized and granular materials coming in contact with the slug. Lime, both air-slaked and hydrated, is the most commonly recommended of these irritants; other materials suggested are salt, caustic soda, tobacco dust, wood ashes, soot, road dust, hellebore, powdered coke, sawdust, and various combinations of these.

Slugs are very often trapped by placing cabbage leaves, straw, culled potatoes, turnips, sacking, or shingles near their favorite haunts in the evening. In the morning they may be easily found and destroyed under these traps, where they have crawled to avoid the daylight. Poison baits of bran, chopped green leaves, drippings, and potatoes, mixed with arsenate of lead, white arsenic, arsenite of zinc, arsenate of calcium, or paris green, as the poison, are said to help in slug control. Fertilizers such as land plaster, nitrate of soda, potassium sulfate, and iron sulfate have been recommended, especially in European countries.

For killing *A. agrestis* by contact or for controlling the slug by a repellent, it has been advised that plants be sprayed with blue vitriol solution, with bordeaux mixture, with pyrethrum, or even with hot water; and as a poison, a spray of arsenate of lead or calcium arsenate is suggested.

It is thus evident that many methods of control have been advised, some of which may work well in a small garden. In a bean field of ten acres or more, with an even infestation thruout, the problem is one of greater complexity.

Experimental work

When this study was begun, in the summer of 1917, the easiest method of control appeared to be the application of a poison spray to the plants. Experiments along this line were started on July 17. Several rows were

TABLE 7. CONTROL EXPERIMENTS AGAINST AGRIOLIMAX AGRESTIS

Material applied	Effect on slugs
Very fine tobacco dust	Dead in 15 minutes
Coarse tobacco dust	Not killed
Builder's lime	Dead in 5 to 15 minutes
Dry powdered bordeaux (dust)	Dead in 5 to 60 minutes
Tobacco dust, sulfur, arsenate of lead (1–5–1)	Dead in 15 minutes
Sulfur (finely ground)	Not killed
Copper sulfate (10-per-cent solution)	Dead in 15 minutes
Copper sulfate (5-per-cent solution)	Dead in 40 minutes
Copper sulfate (2-per-cent solution)	Not killed
Sulfocide (5 cc. to 500 cc. of water)	Not killed
Lime-sulfur (1–20 solution)	Not killed; irritation caused
Black-leaf-40 (1 cc. to 500 cc. of water)	Dead in 2 hours
Quassia solution (hop-aphis formula)	Not killed
Lime (air-slaked)	Dead in 3 to 20 minutes
Washing soda (dust)	Dead in 10 minutes
Chloride of lime (dust)	Dead in 15 minutes
Washing soda (1 pound in 3 gallons of water)	Not killed
Chloride of lime (1 pound in 3 gallons of water)	Dead in 2 hours

sprayed with a mixture of 3 pounds of powdered arsenate of lead to 50 gallons of water. No difference could be noticed between the sprayed and the check plots when they were examined some time later. Slugs were placed also on sprayed plants in cages. Feeding was noticed on the leaves but the animals were not killed. In the greenhouse, in December of 1917, a slug devoured two heavily sprayed plants and lived for many days. From these data it seems evident that ordinary doses of arsenate of lead do not kill *Agriolimax agrestis*.

The experiments summarized in table 7 were carried on in the insectary at Ithaca during the winters of 1917 and 1918. The slugs were sprayed with the liquid or were dusted lightly with the powder, after which they were returned to natural conditions, on moist earth in an open jar.

It may be seen from table 7 that under insectary conditions many dusts proved effective. Copper-sulfate solution also showed strong killing power. It was noticed at this time that a 10-per-cent copper sulfate solution, sprayed on a piece of paper and allowed to dry, was very irritating and sometimes fatal to a slug that crawled across the paper. Lime, chloride of lime, and washing soda were more effective in the form of dust than in the liquid form. Approximately ten slugs were used in each test.

The experiments summarized in table 8 were likewise conducted in the insectary during the winters of 1917 and 1918. Bean plants growing in a bench, and also the ground close to them, were treated with the various liquids and dusts, and a cylinder open at the top was placed over them.

TABLE 8. CONTROL EXPERIMENTS AGAINST AGRIOLIMAX AGRESTIS

Material applied	Effect on slugs
Hydrated lime water (1 pound to 3 gallons)	1 killed, 1 kept from plant for one week
Stone lime (1 pound in 2 gallons of water)	Killed in trying to reach plant
Bordeaux (4–4–50)	Chose unsprayed in preference to sprayed leaves
Arsenate of lead (2 pounds in 50 gallons of water)	Alive after eating two plants
Arsenate of lead, as above, sweetened with molasses	Molasses injured plant
Calcium arsenate (1–50) and sulfocide	Slug not killed; little feeding
Calcium arsenate (1–50) sweetened	Molasses injured plant
Sodium arsenate (10 grams in 1 gallon of water)	Slug alive; plant killed
Check (sprayed with water)	Slug alive
Kansas grasshopper bait	3 of 4 slugs alive 1 week later
Salt and lime (1–10)	Slug killed in 24 hours
Iron sulfate (10-per-cent solution)	Plant killed
Arsenate of lead and lime (1–8)	Slug kept from plant for 1 week
Hellebore and lime (1–25)	Slug killed in 2 hours

One or more slugs were then placed in the cylinder at some distance from the treated plant.

In the experiments summarized in table 8, the repellent effect of bordeaux mixture is shown. Hellebore and lime, as well as salt and lime, showed some killing power under insectary conditions. Calcium arsenate and lead arsenate when sweetened with molasses were fatal to the bean plants, and the ineffectiveness of arsenate of lead as a stomach poison of *A. agrestis* is shown.

In the summer of 1918, contact substances, in powder form, were tried against *A. agrestis* near the field laboratory at Perry. The material was dusted lightly on the slug with a Niagara duster and the animal was then returned to natural conditions. Five slugs were used in each test. The results of some of these experiments are given in table 9:

TABLE 9. EXPERIMENTS WITH POWDERED-CONTACT SUBSTANCES AGAINST AGRIOLIMAX AGRESTIS

Material applied	Effect on slugs
Superphosphate	Killed slowly if extensively used
Rock phosphate	Killed slowly if extensively used
Acid phosphate	Killed slowly if extensively used
Basic phosphate	Not killed
Land plaster	Not killed
Fine ground bone	Not killed
Sulfate of potash	Killed quickly
Nitrate of soda	Killed quickly
Dried blood	Not killed
Ground limestone	Not killed
Calcium cyanamid	Killed rather slowly
Kainit	Killed quickly
Salt	Killed quickly
Sulfur	Not killed
Fine tobacco dust	Killed slowly if extensively used
Chloride of lime	Killed very quickly
Air-slaked lime	Killed quickly
Water-slaked lime	Killed quickly
Salt and lime (1–10)	Killed very quickly
Hellebore and lime (1–10)	Killed very quickly
Hyposulfite of soda	Killed slowly

The nitrate of soda and the kainit proved injurious to the plants when tested in the field. Of the dusts that were not injurious to the plants, as recorded in table 9, the salt-and-lime and the hellebore-and-lime combinations, and the chloride of lime alone, acted the most rapidly, altho some of the other materials also showed killing power.

Liquid-contact materials also were tested in 1918, as shown in table 10. While the slug was crawling on the ground it was sprayed with the liquid from an atomizer, and was then left under natural conditions.

TABLE 10. Liquid-Contact Sprays Tried against Agriolimax agrestis

Material applied	Effect on slugs
Black-leaf-40 (1–400), soap (4–50)	Killed slowly but surely
Limewater (2-per-cent solution)	Killed
Chloride of lime (2-per-cent solution)	Killed quickly
Kerosene emulsion (10 per cent)	Not killed
Kresco sheep dip (10 per cent)	Killed
Carbolic emulsion (1–20)	Killed
Copper sulfate solution (5 per cent)	Killed slowly

In the experiments summarized in table 10, ten large slugs were used to test each material. The Black-leaf-40 was fatal every time, but it often required several hours to kill the slug. The limewater, the chloride of lime, and the carbolic emulsion proved fatal in thirty minutes. The copper sulfate seemed to work much more slowly than in the former tests.

In 1918, during an outbreak at Charlotte, New York, a poison bait composed of one quart of chopped clover, one teaspoonful of arsenate of lead, and one tablespoonful of molasses, was tested. The slugs showed no preference for this bait, and several specimens that were placed where the bait was the only food available, and thus forced to eat it, were not killed.

In July, 1920, the writer was able to find a sufficient number of slugs to enable him to conduct a small series of laboratory tests. The result of these are given in table 11.

In the experiments of 1920, recorded in table 11, both full-grown and immature slugs were used. It was noted that the larger individuals often revived from doses that proved fatal to the smaller specimens. Control materials in dust form seemed to give much better results at this time than did the same material applied as a liquid. In previous experiments sprays have sometimes seemed to give as favorable results as the dusts. There is apparently some varying factor that enters to either help or hinder the killing power of some of these materials. It is possible that the relative humidity may have some influence. Black-leaf-40, which had shown good killing power in the previous experiments, seemed to act very slowly even at the increased strength that was used. Carbolic-acid emulsion gave satisfactory results, and when applied to bean foliage it caused no injury under the prevailing conditions. The best results at this time came from

the contact dusts, but when lime was applied to slugs in the field it was necessary to use several doses before killing resulted. The slug would give off the usual slime, which would mix with the lime to form a coat from which the animal soon freed itself. Heavy doses often killed when light applications did not.

TABLE 11. CONTROL MATERIALS TESTED AGAINST AGRIOLIMAX AGRESTIS IN 1920

Material and strength	Number of slugs	Effect on slugs after 18 to 24 hours
Liquids:		
Black-leaf-40 (1–250), soap (4–100)	25	Small slugs killed if sprayed heavily; large ones revived
Black-leaf-40 (1–250), glue (1 pound to 50 gallons)	10	Small slugs killed; a few large ones revived
Glue (4 pounds to 50 gallons of water)	10	Not killed
Black-leaf-40 (1–250), lime (1 pound to 3 gallons) (light dose)	10	Sick, but all except one revived
Same (heavy dose)	10	All killed
Hydrated lime (1 pound to 3 gallons of water) (light dose)	10	All alive next day
Air-slaked lime (1 pound to 3 gallons of water) (heavy dose)	10	Two large slugs alive; remainder dead
Same (light dose)	10	Five large slugs alive
Lime (1 pound to 3 gallons of water), salt (1.6 ounces to 3 gallons)	10	Five large slugs alive
Lime (8 ounces to 3 gallons of water), chlorinated lime (1.6 ounces to 3 gallons)	10	One large slug alive
Lime (8 ounces to 3 gallons of water), caustic soda (1.6 ounces to 3 gallons)	10	Four large slugs alive; plants burned
Chlorinated lime (8 ounces to 3 gallons of water)	10	Five slugs alive
Carbolic emulsion (diluted 1–30)	10	Killed quickly
Lye (2 pounds to 50 gallons of water)	10	Killed quickly; plants killed
Resin – caustic soda wash (28.3 g. resin, 3.5 g. caustic soda, 645 cc. water)	10	Four small slugs killed
Dusts:		
Hellebore and lime (1–25)	10	All dead
Chlorinated lime and lime (1–25)	10	All dead
Hydrated lime	10	All dead
Niagara Sprayer Company's "All-in-One"	10	All dead
Water-slaked lime	10	All dead
Salt and lime (1–10)	10	All dead
Caustic soda and lime (1–20)	10	All dead
Sulfate of potash	10	All dead; plants burned
Calcium cyanamid	10	All dead; plants burned

Three field cages, containing bean plants sprayed, respectively, with powdered arsenate of lead (2 pounds to 50 gallons of water), calcium arsenate (1 pound of the powder to 50 gallons of water), and water alone to serve as a check, were set up in the laboratory field in July, 1920. Twenty slugs were placed in each cage. The plants sprayed with arsenate of lead were freely eaten, as had been the case in previous experiments; but those sprayed with calcium arsenate showed little evidence of any feeding after the first two days. Several dead slugs were found in the calcium-arsenate cage, while none were found in the arsenate-of-lead cage. The check plants, sprayed with water only, were almost entirely destroyed. The scarcity of slugs in the field had made it impossible to test the calcium-arsenate spray on a larger scale.

A cage was placed in the field covering eight bean plants on July 7, 1920. Four of these plants were sprayed with bordeaux mixture and four were left unsprayed. Twenty slugs were then placed in the cage. A week later the unsprayed plants were badly eaten, while the sprayed plants were almost untouched. Only where a leaf had been missed by the spray was it injured.

Since the above work was carried on, the excellent paper of Lovett and Black (1920) has come from the press. As a result of many careful experiments, these writers conclude that, for Oregon conditions, a spray of bordeaux mixture (4–4–50) as a repellent, supplemented by a poison bait of calcium arsenate (one part by weight to sixteen parts of chopped lettuce), is the most effective means of slug control. When lettuce is not available, cabbage, kale, clover, or other succulent leaves may be used. The writers say that this bait should be scattered in small heaps at frequent intervals over the infested area. The importance of cleaning up crop remnants and débris about fields and gardens is also emphasized. In an experiment testing the efficiency of this combination of repellent and poison bait, Lovett and Black found 33 out of 35 slugs dead at the end of twenty-four hours. The bordeaux had kept the slugs from the plants and they were killed by feeding on the poison bait.

As previously stated, the severity of the winter of 1917–18 apparently killed many hibernating slugs and many slug eggs. Few slugs have been found in New York bean fields since that time, and the writer has not found conditions favorable for control experiments in the field. In 1920 there were more slugs in bean fields than in the two preceding years, but very little injury resulted. The control work has therefore been limited to field-laboratory and greenhouse experiments carried on whenever slugs were available. Results of laboratory experiments have at times been contradictory, and, since laboratory control measures often prove entirely inadequate in field practice, it is impossible at this time to do more than suggest possible control measures for field use under such conditions as those of western New York.

The repellent quality of bordeaux mixture appears to be definitely established. Plants sprayed with bordeaux have escaped all injury when unsprayed plants were entirely devoured. It has been demonstrated by Lovett and Black (1920) that calcium arsenate also has great killing power when used in a poison bait, and the writer found dead slugs in a cage in which the beans had been sprayed with this material. It is therefore reasonable to suppose that a spray of calcium arsenate may be effective under field conditions.

Dusts of lime, salt and lime (1–25), hellebore and lime (1–25), and chloride of lime and lime (1–25), show some promise of success, and on a small scale should work especially well.

A very helpful practice, both in field and garden work, is to remove all rubbish and crop remnants from the ground. Old bean and potato vines, cabbage stumps, carrots, turnips — in fact, decaying vegetation of any kind which may furnish either food or shelter for the slugs — should be cleared away. Straw, boards, roots of quack grass, piles of leaves, and manure, have been found to harbor many of the pests. After a slug infestation, crop remnants should be plowed under or removed from the field as soon as the crop has been harvested. It is advisable also to clean up the edges of gardens and fence corners in the fall if slugs have been abundant during the summer, for the greatest injury to the plants is that caused by slugs hatched from the eggs deposited by overwintering slugs that have hibernated in these places. After the grass and the weeds have been cut and the rubbish has been removed, the application of a heavy coating of lime or salt to the ground helps to destroy the animals.

Beans grown in fields that were in sod the preceding year are often infested. Covered by the roots of the grass, the slugs and their eggs have been well protected during the winter, and when spring comes they find an abundant food supply in the newly planted beans. If manure is added in the fall to sod land in which slugs are present, it makes hibernating conditions even more ideal.

Summary of control suggestions

Bean plants should be thoroly sprayed with bordeaux mixture (4–4–50) to keep the slugs from them. The plants should be sprayed from both above and below, preferably with a potato sprayer having three nozzles to a row. Unless the infestation is severe, this spray should be sufficient. In severe attacks, however, the bordeaux mixture may be supplemented by a bait of chopped lettuce or clover, 16 parts by weight to 1 part of calcium-arsenate powder, the mixture to be scattered around the field. This bait should attract and kill slugs driven from the plants by the bordeaux. As an experiment, the bean foliage may be sprayed with calcium arsenate, 1 pound to 50 gallons of water. In a small garden the slugs

may be collected at night, by the light of a lantern; cabbage leaves, shingles, or straw may be used as traps, from which the slugs may be collected in the morning and destroyed. All crop remnants and rubbish should be carefully removed from infested areas in the fall and destroyed, and salt or lime should be scattered around the edges of the infested fields or gardens. Manure should not be placed on infested fields or gardens in the fall.

HOW TO DISTINGUISH THE VARIOUS SPECIES OF SLUGS FOUND IN BEAN FIELDS

There are three slugs that the writer has frequently found associated with *Agriolimax agrestis*. They are *Agriolimax campestris* Binney, a native species, and *Limax maximus* L. and *Arion circumscriptus* Johnson,[7] imported species. The following key may help in distinguishing the four species.

A. Body blunt or rounded at posterior end; respiratory opening in anterior half of mantle; back not keeled in mature forms; color gray, with a black lateral band the entire length of body; length 30 mm ..... *Arion circumscriptus*

B. Body pointed at posterior end; respiratory opening in posterior half of mantle; back with at least a small keel at posterior end; color varied, but without the single lateral stripe.

a. Slug large (100–200 mm.); spotted or with longitudinal bands of black. *Limax maximus*

b. Slug smaller (25–50 mm.); color uniform or mottled.

aa. Ground color usually whitish or ocherous, mottled or speckled with brown or black; mantle pore with unpigmented border; tubercles flattened; slime milky; length when full-grown, 50 mm ..... *Agriolimax agrestis*

bb. Color uniformly amber or black; mantle pore of same color as remainder of mantle; tubercles not flattened; slime watery; length when full-grown, 25 mm ..... *Agriolimax campestris*

Agriolimax campestris Binney

Animal limaciform, with large, not flattened, tubercles. Color uniform grayish or amber, often black. Body somewhat compressed and keeled toward the caudal end. Tentacles dark-colored. Shield more than one-third total length of animal, rounded in front and behind. Respiratory orifice not differing markedly in color from remainder of mantle. Sole dark and longitudinally tripartite. Mucus clear and watery. Penis spiral. Length about 25 mm.

Agriolimax campestris, a native species, is closely related to *A. agrestis*. It differs from *agrestis* in being smaller, darker, and of a more uniform coloring. While *agrestis* seems to collect in large numbers and to thrive on cultivated crops, *campestris* is more inclined to be solitary and to frequent woods and meadows. In April, full-grown *campestris* are often found under stones or in sod, and the eggs have been found at the same time. Eighteen of these eggs, taken on April 22, hatched between May 21 and June 1. The young of *campestris* are darker than the young of

[7] Determined by H. A. Pilsbry.

agrestis, some being almost black. It is not uncommon to find *campestris* feeding on beans, but they never occur in numbers large enough to seriously damage the crop.

The spotted garden slug, Limax maximus L.

Limax maximus (Plate LXX, 6), is described by Taylor (1907:35) as follows:

> Animal with a long and slender body, tapering towards the tail, and varying in length from 100 to 150 mill., but occasionally reaching to even 200 mill.; usually of a yellowish-grey or cinereous ground colour, variously banded or maculated with black, but sometimes unicolorous; body rounded, but keeled towards the caudal end, with about forty-eight longitudinal rows of elongate, detached tubercles; neck pale, with two conspicuous dorsal furrows enclosing a single row of elongate tubercles and terminating in front as the facial grooves; sole uniformly pale; foot-fringe pale with a row of minute submarginal blackish tubercles; tentacles very long and slender; shield oblong, about one-third the total length of the animal, rounded in front, angular behind, and forming an angle of about 80 deg. when in motion, usually of a similar tint to the body, but boldly marbled or maculate with black, somewhat concentrically and interruptedly ridged around a sub-posterior nucleus. Mucus colourless and ridescent, not very adhesive.....

Limax maximus is a large slug, of the family Limacidae, which has been imported into this country. It is found in the British Isles, and thruout Continental Europe, South Africa, and Australia. It has been in America for many years and may be found locally in many parts of New York State, where it frequents greenhouses, hedgerows, woods, and damp, shady places. It occurs also in and around houses occasionally, when it has been carried in on vegetables that are stored in the cellar. Taylor (1907) states that the slug is almost omnivorous, having been known to relish beans, tobacco, flowers of many kinds, cauliflower, fungi, custards, milk, bread, raw and cooked meat, fruit, and sugar.

L. maximus has a keen sense of smell. It has been known to crawl, in the dark, straight to a plate of meat that was six feet away. The position of the plate was then changed three times, and each time the slug altered its course accordingly. It is said that *L. maximus* often returns to the same spot night after night, after its wanderings in the dark. The progress of the night's journey is shown by the slime trail which is left wherever the animal goes.

Arion circumscriptus Johnson

The following description of *Arion circumscriptus* (Plate LXIX, 12) is taken from Taylor (1907:228):

> Animal of the *Arion* shape, but stouter especially when contracted.....about thirty mill. in length when adult and fully extended; of a pale creamy-grey colour, darker grey dorsally, but shading to whitish towards the fringe; a black and sharply-defined lateral band extends the whole length of the body on each side, beneath which is sometimes an indistinct orange band, formed by pigment cells breaking through the skin; there is a slight mid-dorsal keel when young, which, however, gradually disappears during growth, but its place is almost

invariably indicated by a line of pale mid-dorsal tubercles, which contribute to form a pair of dorsal or inner bands; shield granulose and bluntly rounded at both ends, bearing a disconnected continuation of the longitudinal body banding; body tubercles rather long and slender; sole opaque, waxy white, and indistinctly tripartite, the median portion slightly darker and more transparent than the side areas, and occupying more than one-third of the width of the body; foot-fringe broad and white or pale-grey in colour, usually without perceptible lineolations, but sometimes the lineoles are clearly pigmented, especially at the caudal end of the body.

Another slug occasionally found with *Agriolimax agrestis* in New York is *Arion circumscriptus* Johnson, a species imported into this country from Europe and reported by Taylor (1907) from Niagara Falls and from the District of Columbia. The writer has found it very common at Ithaca, at Perry, and at Waterville, in New York. This slug apparently prefers to live in sod land, in decaying tree trunks, or under fallen leaves. It may be found in grassy orchards, feeding on bruised and decaying fruit. It is seldom, if ever, injurious to growing plants. The species belongs to the family Arionidae. It may be easily separated from the other slugs found with *Agriolimax agrestis* by the position of its respiratory pore, which is in the anterior half of the mantle while in the other forms it is in the posterior half. A longitudinal black band runs the full length of the animal's body.

THE PALE-STRIPED FLEA BEETLE

(*Systena taeniata* Say)

The pale-striped flea beetle, *Systena taeniata* (of the family Chrysomelidae), is found in the bean fields in New York State every year, in large or small numbers. This small, active insect is brownish yellow in color, with a broad yellow stripe running lengthwise along each wing cover (Plate LXIX, 11). There are several color varieties of the insect, but the common one in New York is *blanda*, in which there is little contrast between the stripe and the remainder of the wing cover. The typical dark form is found occasionally. In early writings these varieties were often treated as separate species. When *S. taeniata* is numerous in dry summers, the beetles may cause considerable injury to beans by attacking the foliage. They leave in their wake many shallow feeding places on the surface of the leaves, and some of these spots later develop into irregular holes. If the plant is unable to supply sufficient soil water for the increased transpiration resulting from the injury, the leaves will turn a sickly yellow. In a year when the normal supply of soil moisture is available, beans can sustain much damage from the feeding of the insect without any serious injury resulting to the development of the plant.

S. taeniata is a well-known insect in nearly all parts of the United States, and in many places is considered a serious pest. It has injured sugar beets in Michigan, in New York, and in Colorado, corn in Illinois, clover in Kentucky, cotton in Georgia, Kieffer pear grafts in Maryland, and seedling apple trees in New York. Other host plants of the insect are

cabbage, potato, pea, tomato, pumpkin, melon, squash, cucumber, turnip, radish, carrot, eggplant, strawberry, blackberry, lettuce, sweet potato, summer savory, peanut, sunflower, oak, timothy, and oats. It is reported by Chittenden (1900) and other writers as occurring also on the following weeds: ragweed, lamb's-quarters, pigweed, Jamestown weed, cocklebur, black, or garden, nightshade, purslane, fleabane, sand bur, and other plants. The writer has found it on mustard and daisy.

Every time that *S. taeniata* has been found on beans in New York, some of its common weed hosts have been near by. Ragweed and lamb's-quarters appear to be its favorite food plants.

DESCRIPTION OF STAGES

The egg

The egg of *Systena taeniata* (Plate LXX, 3) is elliptical, slightly more rounded at one end, is pale yellow n color, and has a roughened surface. Under the high power of the microscope, the egg covering is seen to be divided into a definite pattern of depressed hexagonal areas, with irregular reticulations in the hexagons. Under a lens it appears faintly roughened. Its length is from 0.6 to 0.65 millimeter.

The larva

The larva (Plate LXIX, 8) is described by Forbes (1894) as follows:

> Length 5 mm., greatest width about .6 mm. Slender, widening gradually to the 11th segment, thence tapering quite rapidly. General color pale yellow or brownish yellow, paler towards the posterior end. Head yellowish brown, with numerous stiff hairs; jaws darker brown. Antennae three-jointed, pale, short, and thick. The thorax and abdomen are darkest on the dorsum, fading to paler on the margins and ventral surface, and the latter very pale yellowish at the end. The first thoracic segment has two longitudinal curved impressed lines on the dorsum; segments two and three have longitudinal impressed lines on each side near the border, between which is a transverse curved line crossing each segment near its anterior margin, from which two oblique straight lines extend to the posterior margins of the segments. The legs have stout, blunt, spine-like processes on their anterior surfaces, and stiff hairs on the posterior. The abdominal segments are transversely wrinkled on both anterior and posterior margins. The skin is shagreened, and the whole body is supplied with stiff, spine-like hairs of various lengths. The anal segment has a single fleshy proleg. When seen from above this segment rapidly narrows to midway its length, the posterior half forming a rounded, lobe-like projection of about one half the width of the anterior portion of the segment. On the projection are four long, stiff, spine-like hairs and a marginal crown of shorter spine-like processes, each of which ends in a fine, curved, hair-like lash. (Described from two specimens.)

The pupa

The pupa (Plate LXIX, 9) is pale yellow in color until just before the emergence of the adult beetle, when the darker body markings may be seen thru the pupal skin. The end of the body bears two heavy, prominent, slightly incurving spines. The length is about 4 millimeters.

The adult

The adult (Plate LXIX, 11) is described by Blatchley (1910) as follows:

Elongate-oval. Color variable, usually reddish or brownish-yellow, shining; elytra each always with a paler median stripe; under surface and narrow margins of thorax usually piceous; antennae and legs reddish-brown. Thorax one-fourth wider than long, sides feebly rounded, surface finely and sparsely punctured. Elytra distinctly wider than thorax, finely, shallowly and rather densely punctate. Length 3–4.5 mm.

LIFE HISTORY AND HABITS

The egg

Eggs of the pale-striped flea beetle were nearly mature in dissected females on July 15, 1919, and beetles placed in a cage with ragweed and beans on that date had deposited eggs in the soil by July 22. In 1920 no eggs were found in females opened on June 29, but they were present in specimens opened on July 21. In the cages eggs were deposited for some time after August 6; many were deposited about August 25, and some could still be found on September 8. It may be said that in New York the period of oviposition of *Systena taeniata* extends from the last of July until the first part of September.

In 1919, after finding eggs of *S. taeniata* in cages the writer looked for them in the field, and on July 29 a few were discovered around ragweed. On August 5 some were taken near the roots of lamb's-quarters, and later many more were found around this host. Nineteen eggs under observation in the laboratory hatched in an average of 17 days, with a range from 15 to 23 days.

The egg of *S. taeniata* closely resembles that of *S. frontalis*, which is frequently present in the same habitat, and sometimes it is difficult to distinguish the eggs of these two species. However, the eggs of *taeniata* are smaller and are deposited earlier in the season than those of *frontalis*. Few females of *frontalis* were mature when eggs were found in the field on August 5, and, since a dead specimen of *taeniata* was found in the ground near these eggs, there is little doubt of their parentage.

Eggs of *taeniata* are usually scattered in the ground singly, but they may occur in clusters of from two to seven. They may be found from half an inch to three inches deep, and the writer has always found them near the roots of ragweed and lamb's-quarters tho they no doubt occur also near some of the other hosts of the insect.

The larva

Eggs of *Systena taeniata* have hatched in the laboratory from July 25 to September 8. The newly hatched larvae feed below ground on the roots of their weed hosts. A few small larvae, together with eggs of this species, were found on the lateral roots of lamb's-quarters in August, 1919. Larvae of this species have not been found feeding on the roots of beans.

The writer has not succeeded in rearing these larvae, but it is believed that the insect hibernates in the larval stage near the roots of its host plants. On May 25, 1920, larvae of what is believed to be this species were found around ragweed, but when these were taken to the laboratory for rearing, they died. Later, pupae of *S. taeniata* were found in this same place. It seems reasonably certain, then, that the larval stage normally begins between the last of July and the middle of September, and does not end until late May or early June of the following year. This would make a larval period of from nine to eleven months. In 1886 Forbes (1894) found larvae feeding in young corn plants in Illinois on May 17, and again on July 11 and 12. Chittenden (1903) reports finding larvae feeding on the roots of lamb's-quarters and Jamestown weed.

The pupa

Pupae of *Systena taeniata* were found from June 29 to July 12, 1920, around dead ragweed along the edge of a field that had been in beans the previous year. Twenty were discovered about one plant, three inches below the surface, in rather compact soil. Beetles emerged from these pupae between July 13 and July 25. Forbes (1894) reports pupae emerging on May 26 and June 7 from larvae found on May 17. Adults from these pupae emerged by June 17. It would appear, then, that the pupal stage may cover from two to three weeks.

The adult

Pale-striped flea beetles have been taken in the field from the middle of June until the middle of September. In 1920 the first beetle was seen on June 19 and a few were alive in cages on September 10; the maximum number was present on plants about July 20. The ovaries of female beetles opened on June 29 were very immature, but many well-developed eggs were found in insects dissected on July 21.

It has been noticed each year that when *Systena taeniata* becomes scarce on beans, beetles may still be found on ragweed and lamb's-quarters, especially along the edges of fields. On August 19, 1920, *taeniata* was becoming scarce on beans, but it occurred in large numbers on its weed hosts until about September 3.

During the latter part of their adult life, the females go down into the ground around their favorite food plants to deposit their eggs. In searching for eggs, the writer has often found the beetles crawling in the dirt three inches below the surface. One much battered female was found four inches down in the ground, near a ragweed plant, on September 16, 1919, when most of the beetles had disappeared. On September 23, 1919, a beetle with particles of dirt adhering to its legs and its wing covers was found on ragweed. It had apparently been down in the ground, had deposited its eggs, and had come up again to feed.

The parent beetle of *S. taeniata* lives for a relatively long time and the period of oviposition covers a month or more. Beetles have been seen in copulation from June, when the ovaries were still immature, until September, when nearly all the eggs were deposited. Since the period of egg laying may vary so greatly, it seems likely that some beetles which emerge late in the summer and continue to oviposit for a long time may pass the winter in the beetle stage. Chittenden (1903) states that the insect hibernates as an adult, and Gibson (1913) found overwintering beetles in timothy fields in Ontario (Canada) in May. There is therefore good evidence of adult hibernation in some places, but the writer believes that this is rare in New York. Forbes (1905) believes that in Illinois the insect hibernates as a larva, and the writer's observations point to the same conclusion for New York. Chittenden (1900) believes that there may be a second brood at Washington, but the writer believes that in New York there is only one brood.

SEASONAL HISTORY

The parent beetle of *Systena taeniata*, emerging during June and July, deposits eggs in the ground around ragweed, lamb's-quarters, and possibly other hosts, from July to September. These eggs hatch in from two to three weeks, and the larvae hibernate after feeding for some time on the fine roots of their host plants. During June and July of the next year these larvae emerge as pupae, and after two or three weeks the beetles appear. In New York there is only one generation a year.

CONTROL

Clean cultivation is an important factor in the control of *Systena taeniata*. Fence corners and the edges of fields, which are never cultivated and where ragweed and lamb's-quarters flourish, often become centers of infestation. The pupae of *taeniata* have been found in large numbers around these weeds at the side of a field that had been in beans the preceding year. In this field the beetles were first seen near these weeds in the spring, and thruout the summer, when beans were again planted, the insects were more numerous along this border of the field. When the female beetles are mature they seek out these weed hosts as places for oviposition. The careful eradication of these weeds from the side of the fields and from among the bean plants will help greatly in reducing the numbers of the insect. Eggs are often deposited near weeds growing in the field proper, but it is probable that many larvae and pupae are destroyed when the ground is fitted for the following crop. If these weeds are removed from a field and from its environs late in August, when most of the eggs are deposited, the young larvae will be without food and many will die. One grower planted beans in the same field for several succeeding years, and there were always many *taeniata* present on his plants. Early in September, 1919, he pulled out all of the ragweed and lamb's-quarters growing in the field proper, as well as that along the margin, and in 1920 not more

than one-fourth as many flea beetles were present as there had been the year before. The food supply of the young larvae was removed at a critical time, apparently causing many to die of starvation.

The parent beetles are often numerous on ragweed and lamb's-quarters growing among wheat and oat stubble in the fall; and it has been noticed that when beans were planted in these fields the following year, the beetles were often abundant. Beans grown on land that had previously been in clover in which some ragweed had also sprung up, often show as heavy an infestation of *S. taeniata*. If sod land or stubble land of this type is plowed deep in September, when the larvae are small, so as to destroy the larval food supply, it is probable that the infestation of the following spring will be much reduced.

Artificial control measures tested against *S. taeniata* and the red-headed flea beetle, *S. frontalis*, are discussed on page 1009.

FIG. 93. BEAN PLANTS DAMAGED BY THE RED-HEADED FLEA BEETLE

A few beetles may be seen on the plants

THE RED-HEADED FLEA BEETLE

(*Systena frontalis* Fab.)

A rather large, black flea beetle, with a red head, *Systena frontalis* (of the family Chrysomelidae), may be found more or less abundant in bean fields in New York every year. In dry seasons it is often numerous enough to cause considerable damage to the foliage (figs. 93 and 94). This insect has been found at Perry, New York, each year since 1917, and in 1918, when there was little rain, many beans turned yellow as a result of the feeding of this species and the closely related form, *S. taeniata*. Thirty beetles have been counted feeding on the upper surface of the leaves of a single plant. They often congregate on a few plants, seriously damaging them, while other plants are almost free from the pests.

S. frontalis is a common insect in the United States east of the Rocky Mountains, and in parts of Canada. It has been reported as injurious to grapes, cabbage, beets, potatoes, corn, beans, clover, cranberries, gooseberries, mangle-wurzels, and pear leaves. It is known to occur also on

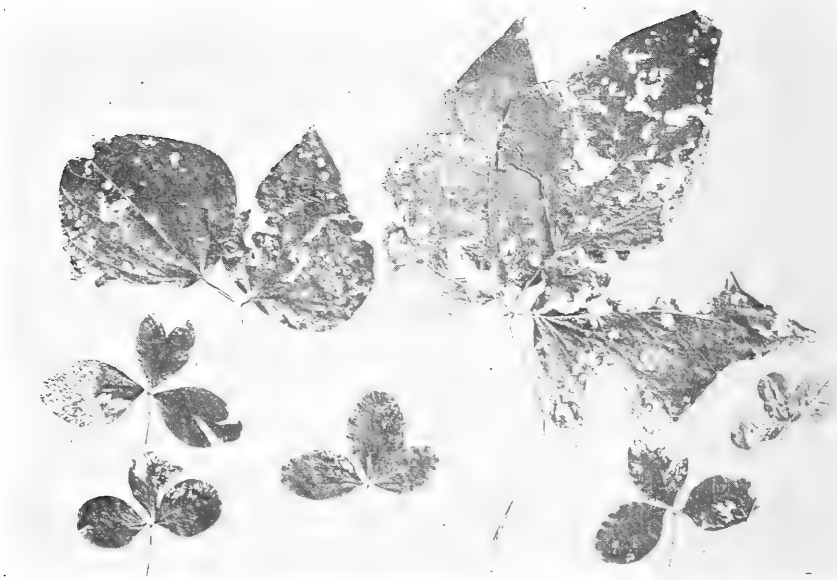

Fig. 94. BEAN AND CLOVER LEAVES INJURED BY THE RED-HEADED FLEA-BEETLE

Japanese honeysuckle, weigela, aster, chrysanthemum, marsh mallow, rose mallow, smartweed, pigweed, lamb's-quarters, and ragweed. In addition to these hosts, the writer has found the species on goldenrod, daisy, broad-leafed plantain (*Plantago major* L.), black bindweed (*Polygonum convolvulus* L.), common burdock (*Arctium minus* Bernh.), heal-all (*Prunella vulgaris* L.), lady's-thumb (*Polygonum Persicaria* L.), wild lettuce (*Lactuca canadensis* L.), and beggar-ticks (*Bidens frondosa* L.).

Where *S. frontalis* has been found in large numbers, some of its weed hosts also have been abundant. Ragweed, lamb's-quarters, and beggar-ticks seem to be the most preferred.

DESCRIPTION OF STAGES

The egg

The egg of *Systena frontalis* is elliptical, slightly more rounded at one end, and is pale yellow in color (Plate LXXI, 6). The surface is roughened. Under high power these roughened areas are seen to be irregular, and they are made by the union of shallow grooves which form the borders of differently shaped polygons. The length is from 0.7 to 0.85 millimeter.

The larva

The larva (Plate LXIX, 7) is dirty white in color, appearing darker where the contents of the alimentary canal show thru the body. The largest diameter is at a point about two-thirds of the distance to the caudal end. The head is pale yellow, with darker markings on the lateral aspect near the lower side. The body is much wrinkled and is covered with many setae. On the caudal end there is a prominent erect tubercle bearing two pairs of prominent spines, and on the apex a tuft of fine hairs. An anal proleg is present. This description is from one specimen, 5.5 millimeters in length and probably nearly mature.

The adult

The adult (Plate LXXI, 8) is described by Blatchley (1910) as follows:

Resembles *hudsonius* very closely. Usually a little broader and less shining, the head reddish or reddish-yellow; antennae and legs mostly pale. Thorax more distinctly and elytra less coarsely punctate. Males in both species with the last ventral segment notched each side, the middle lobe with a deeply impressed triangular median line. Length 3.5–4.5 mm.

LIFE HISTORY AND HABITS

The egg

Immature eggs of *Systena frontalis* were found in dissected females on July 15, 1919. A few mature eggs were found in insects opened on August 5, and many were found in those dissected on August 18. From this time until September 15, eggs were found in beetles that were opened. Eggs deposited in the cages were found after August 6. In 1920 the insects were much later in appearing. The first beetles were taken on July 29, and specimens containing mature eggs were scarce until September 3. Most of the oviposition in the cages occurred early in September. It may be said, then, that the oviposition period varies greatly from year to year, occurring at any time in August or September.

After finding eggs in the laboratory cages, the writer searched for them in the field, and on September 20, 1919, a few were found around ragweed and lady's-thumb After that date, eggs were frequently found on the soil near ragweed, and on September 5 three eggs were located near beggar-ticks. On September 11, eggs were found near a bean plant in a field where ragweed was growing among the beans, and in the same field, on September 15, one egg was discovered near a plant of lamb's-quarters. As previously stated, the eggs of *S. frontalis* and those of *S. taeniata* are very similar, but the eggs of *frontalis* are larger and are usually deposited later in the season than those of *taeniata*. The eggs of *taeniata* hatch in the fall, while *frontalis* winters in the egg stage. The eggs just mentioned as having been found in the fall of 1919 did not hatch that fall.

Eggs of *frontalis* have been found, in the field, scattered irregularly about the roots of its host plants and from one-half to two inches deep.

Most of the eggs found have been near ragweed and beggar-ticks, tho a few have been found near other hosts.

The eggs of *S. frontalis* that have been under observation have never hatched during the same year in which they were deposited. Eleven eggs deposited on August 24, 1919, hatched between May 20 and 26, 1920. These eggs were kept during the winter on moist dirt in a petri dish in a cool room. Eggs deposited during September, 1920, and kept in a warm office, had not hatched by February 20, 1921. It would seem, therefore, that the egg stage of this insect covers about nine months. Scammell (1917) says: "Egg laying begins in late July, with deposition just below the surface of the ground. Hatching takes place the following May."

The larva and the pupa

Little is known of the larval stage of *Systena frontalis*. Two larvae hatching on May 25, 1920, were reared until June 15. At that time the larger one had reached a length of 5.5 millimeters and was probably nearly full-grown. The writer did not succeed in rearing these larvae thru to pupae. The larval stage is probably passed in feeding on the roots of the insect's weed hosts, but there are no definite data on the larval and pupal parts of the life history. A pupa believed to be that of *frontalis* was found near beggar-ticks in June, 1920, but as it could not be reared the identity is uncertain.

The adult

The red-headed flea beetles have been taken in the field from early in July until the first of October. They are most abundant on beans in August. Beetles have frequently been seen in copulation during August, and in 1920 some were observed as late as September 15.

Blatchley (1910) found the parent beetles of *Systena frontalis* wintering beneath the bark of white maple and in mullein, in Indiana. The writer has not succeeded in keeping the caged beetles alive thru the winter in New York, and, since this insect has not been found in the spring before July, it is doubtful that it hibernates as an adult in this State.

Red-headed flea beetles caged with ragweed or beans will feed actively for a few days and then go into the ground to deposit their eggs. In the field the same condition is found. After feeding on beans they move to ragweed, beggar-ticks, or some other host, where they may be found in numbers until they go into the soil for oviposition.

SEASONAL HISTORY

The parent beetle of *Systena frontalis* comes from the ground in July and August, and, after feeding on its cultivated and weed hosts, enters the ground for oviposition during August and September. The eggs overwinter near the plants, and hatch in May of the following year. The larval

and pupal stages are little known, but the larvae probably feed on the roots of ragweed, beggar-ticks, and other weeds, pupating sometime in June.

CONTROL

It has been pointed out that clean cultivation is an important factor in the control of *Systena taeniata*, and this is equally true for *S. frontalis*. The removal of ragweed, lamb's-quarters, and beggar-ticks from a field

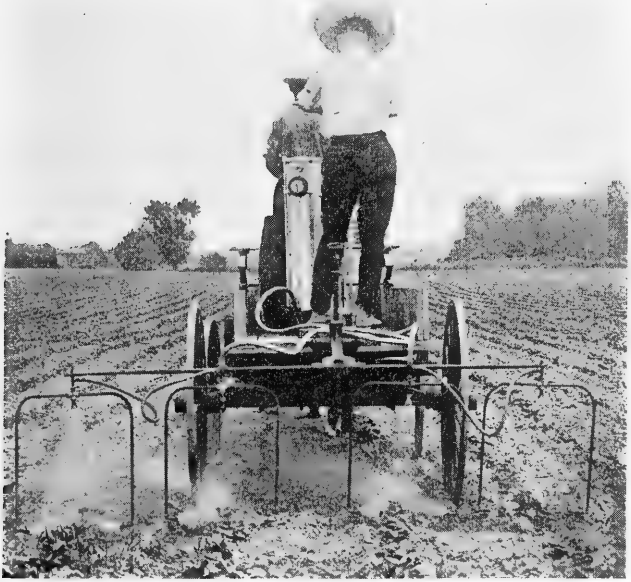

Fig 95. SPRAYING MACHINE USED IN EXPERIMENTS FOR THE CONTROL OF FLEA BEETLES ON BEANS

after the eggs have been deposited in the fall and again before they hatch in the spring, should destroy many of the pests. Many of the insects breed along the edges of fields and in overgrown fence corners, and therefore keeping the weeds cleaned up in these places is a great help in reducing the number of beetles that may emerge.

In the summer of 1919, red-headed flea beetles were numerous in a bean field just across the road from the Perry laboratory, and control experiments were conducted there. On July 18, bean plants were sprayed with arsenate of lead (3 pounds of paste to 50 gallons of water), and twenty-five beetles were placed in a cage over these plants. The same number of

TABLE 12. CONTROL MEASURES TESTED AGAINST SYSTENA FRONTALIS ON BEANS IN 1919

Row	Material, and method of application	Date of application	Length of row examined on July 17 (yards)	Number of *S. frontalis* present on July 17		Length of row examined on July 19 (yards)	Number of beetles present on July 19			
				Total number	Number per yard		*S. frontalis*	*S. taeniata*	Total number	Number per yard
26	Check	.....	35	74	2.11	23	37	6	43	1.89
28	Lime — 1 pound to 2 gallons of water; compressed-air sprayer	July 16	74	14	0.18	74	32	1	33	0.44
29	Check	.....	35	57	1.63	26	48	8	56	2.15
31	Fish-oil soap — ½ pound to 2 gallons of water; compressed-air sprayer	July 16	133	16	0.12	133	59	10	69	0.52
32	Check	.....	37	70	1.89	133	131	14	145	1.09
34	Sulfur — 1 pound to 2 gallons of water; compressed-air sprayer	July 16	88	8	0.09	84	35	3	38	0.45
35	Check	.....	46	67	1.45	26	36	7	43	1.65
37	Arsenate of lead paste (3–50); compressed-air sprayer	July 16	60	5	0.08	55	8	0	8	0.14
38	Check	.....	40	66	1.65	40	23	3	26	0.65
39	Bordeaux (5–5–50), arsenate of lead (3–50); barrel pump on wagon	July 14	90	6	0.06	288	17	1	18	0.06
40	Same as on row 39	July 14	.....	.....	.....	288	21	4	25	0.08
44	Check	.....	79	96	1.21	23	15	4	19	0.82
46	Arsenate of lead paste (3–50); barrel pump on wagon	July 17	.....	.....	.....	84	6	2	8	0.09
47	Same as on row 46	July 17	.....	.....	.....	84	5	1	6	0.07
48	Check	.....	.....	.....	.....	34	24	2	26	0.76
50	Land plaster; dusted on plants	July 18	.....	.....	.....	66	56	15	71	1.07
51	Check	.....	.....	.....	.....	25	31	13	44	1.76
53	Lime; dusted on plants	July 18	.....	.....	.....	54	25	12	37	0.68
55	Check	.....	.....	.....	.....	21	24	13	37	1.76
56	Basic phosphate; dusted on plants	July 18	.....	.....	.....	34	16	6	22	0.64
57	Check	.....	.....	.....	.....	20	21	4	25	1.25
59	Fine ground bone; dusted on plants	July 18	.....	.....	.....	26	9	9	18	0.69
61	Check	.....	.....	.....	.....	28	12	10	22	0.78
62	Superphosphate; dusted on plants	July 18	.....	.....	.....	30	13	15	28	0.93
64	Check	.....	.....	.....	.....	28	18	6	24	0.85
65	Sulfur; dusted on plants	July 18	.....	.....	.....	64	10	1	11	0.17
66	Check	.....	.....	.....	.....	41	17	9	26	0.63
68	Tobacco dust; dusted on plants	July 18	.....	.....	.....	62	15	4	19	0.30

Average of checks, 1.36 beetles per yard

beetles caged over unsprayed beans served as a check. On July 24, eighteen of the twenty-five beetles were alive in the check cage but no live beetles could be found in the cage where arsenate of lead had been applied. Field experiments tested on a larger scale are listed in table 12.

For the experiments recorded in table 12, 94 rows of beans were planted in the field, running from east to west. At least one check row was left alternating with the treated rows. A compressed-air sprayer was used in some of the experiments, but in treating rows 39, 40, 46, and 47, a hand pump on a wagon (fig. 95), with a spray boom feeding twelve nozzles and covering four rows, was used. It was impossible to keep up sufficient pressure to feed all of the nozzles with this pump, and so the outfit would be unfit for practical work unless the boom was attached to a power sprayer or to an efficient traction machine. The three nozzles to a row covered both the upper and lower surfaces of the bean leaves. At this time the plants were still very small, but it is quite possible to spray beans when the vines are more developed. A small hand machine operated by a crank was used in applying the dusts.

Of the materials tested, the bordeaux-arsenate-of-lead spray gave the best results, but arsenate of lead alone was nearly as effective. It is apparent that arsenate of lead has good repellent qualities in addition to its killing power. Sprays of limewater, sulfur, and fish-oil soap also repelled the beetles, tho to a less extent; and several of the fertilizers dusted on the plants kept off some of the insects.

If beans become heavily infested with flea beetles in July, when the plants are small, and if growth is slow because of dry weather, spraying with the bordeaux-arsenate-of-lead mixture or with arsenate of lead alone is beneficial. If suitable machinery is not available for spraying, the plants may be dusted with lime or with a combination of arsenate of lead and lime. In all cases the wild hosts should be removed from fence corners, from the sides of the field, and from the field itself, soon after oviposition is finished in September.

THE GREEN CLOVER WORM

(*Plathypena scabra* Fab.)

During July and until October of 1919, the green clover worm (*Plathypena scabra*, (Lepidoptera, Noctuidae) was very common on field beans in New York. The larvae of this snout moth may be found in small numbers on beans in almost any year, but only occasionally is it a serious pest. In 1917 and 1918 the writer found only four larvae of this species on beans.

Among the many hosts of the green clover worm are beans, lima beans, soybeans, peas, cowpeas, vetch, clover, alfalfa, strawberry, blackberry, tickweed, ragweed, smartweed, and wild carrot. The larvae that have been found on field beans in New York apparently belong to the second

generation. As the early-season hosts were not seriously injured, the first generation no doubt developed unnoticed and the pest appeared on beans in midsummer greatly augmented in numbers.

The green clover worm usually hibernates as a moth (fig. 96, B). In the fall the parent insect crawls into strawstacks, into barns, under the bark of

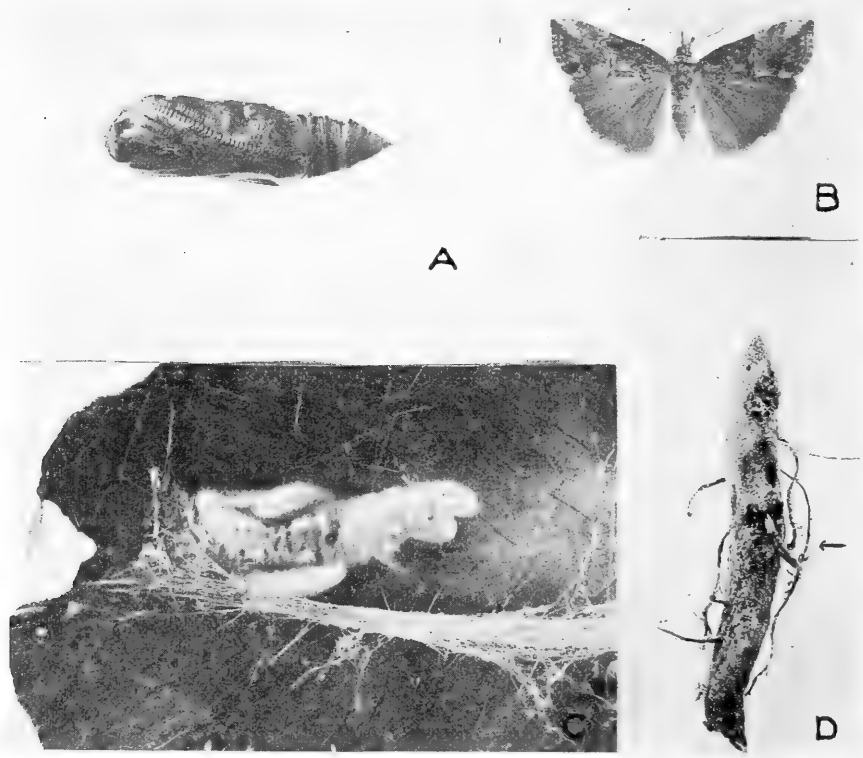

FIG. 96. PLATHYPENA SCABRA AND AGRIOTES MANCUS

A, Pupa of *Plathypena scabra*, × about 3. B, Female moth of *P. scabra*, slightly enlarged. C, Larva of *P. scabra* parasitized by larvae of *Rhyssalus loxoteniae*, enlarged
D, A larva of *Agriotes mancus* entering a diseased bean root, slightly reduced

trees, or to any place where it may be protected from the cold. It is probable that under normal winter conditions a large proportion of these moths die before spring, but the winter of 1918–19 was so mild that the number of insects emerging from hibernation the following spring was far above the average. The mean temperature at Ithaca for the months of December, 1918, and January and February, 1919, averaged 11 degrees higher than

for the corresponding months of 1919–20. In the summer of 1920, which followed an unusually severe winter, the writer could find only one larva of this pest. This was a parasitized specimen (fig. 96, C) found on June 3 on clover, from which eight specimens of *Rhyssalus loxoteniae* Ashm.[8] were reared. From a larva taken on beans on August 22, 1919, another parasite, *Aleiodes intermedius* Cress.,[8] emerged on September 4

When undisturbed, the larva of *Plathypena scabra* rests quietly on the leaf and is inconspicuous by reason of its pale green color (fig. 97, B); but when the plant is shaken, the larva may drop to the ground and squirm back and forth for some time, or it may remain suspended in mid-air by a fine silken thread. The older larvae are voracious feeders. They eat entirely thru a leaf (fig. 97, A), and sometimes make large holes in the pods (Plate LXX, 5).

The pupa (fig. 96, A) is mahogany

FIG. 97. WORK OF THE GREEN CLOVER WORM

A, Bean leaves injured by feeding of the worm, reduced. B, Larva feeding on a bean leaf, slightly enlarged

[8] Determined by C. F. W. Meusebeck.

brown in color, is about 12 millimeters in length, and bears several hook-like spines on the end. This stage of the insect is usually passed above or below ground in a frail cocoon covered with particles of dirt.

The moths of *P. scabra*, reared from larvae found on beans at Perry in July, emerged in cages from August 25 to October 1. Late in September there were many moths in the fields around the piles of drying beans. No eggs were deposited by moths in cages before they were killed by cold weather.

The larvae found in a field at any one time vary greatly in size, and some larvae could still be found when moths were seeking hibernating places. On September 9 larvae of all sizes were taken on beans, and more were found on ragweed on October 2. It seems probable that there are normally two broods of this insect in New York, but that in long warm summers there may be a partial third brood.

When the larvae of *P. scabra* appear in such large numbers that they threaten the bean crop, they may be controlled by a spray of arsenate of lead, 2 to 3 pounds of paste to 50 gallons of water. To insure the destruction of all larvae, the under as well as the upper sides of the leaves should be covered. Sherman and Leiby (1920) found that the pest could be controlled when feeding on soybeans by dusting the plants with a combination of 1 part of powdered arsenate of lead to 8 parts of lime. The material must be applied as soon as the insects begin their work. A hand duster, geared to distribute two pounds to the acre, is recommended by these writers.

On wax and string beans it is not always safe to apply a poison to the pods. To kill the insects on plants of this type, a spray of Black-leaf-40 (1 gallon to 750 gallons of water), with the addition of soap (3 pounds to 50 gallons of water), should be used. For small gardens, a mixture of one teaspoonful of Black-leaf-40 and one ounce of laundry soap in one gallon of water has been found effective. As the larva is killed only when thoroly drenched by the spray, it is necessary to cover both the upper and the under sides of the leaves.

THE BEAN WEEVIL

(*Acanthoscelides* [*Bruchus*] *obtectus* Say)

There is no other bean pest as well known and as much discussed in entomological literature as the bean weevil, *Acanthoscelides obtectus* (Coleoptera, Bruchidae) (fig. 98). It is not a field pest in New York, but, since it frequently causes great loss to beans in storage, a brief discussion of it may be justified in this paper.

When beans that have been infested in the field are kept in a warm storeroom, the reproduction of the weevil continues, and generation after generation develops in the stored seed. The same thing may happen when uninfested beans are put in a warm place where the weevils are already

present. This work in stored beans is the only loss occasioned by this insect in New York (Plate LXXI, 3).

In an effort to determine the summer habits of the weevils that emerge from infested seed when it is planted, the writer, on June 18, 1918, placed weevils, and beans containing larvae and pupae of the insect, in a field cage in which small bean plants were growing. On July 2 it was noted that the parent beetles had eaten small pieces from the leaves of the plants; and on August 15 the beans just below the surface of the ground, that had not germinated, were filled with larvae, pupae, and adults of the insect. This condition still prevailed on October 1.

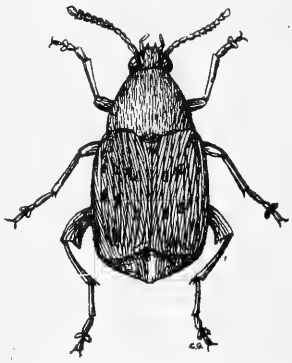

Fig. 98. The bean weevil, Acanthoscelides obtectus

Bean weevils are not a serious pest under New York conditions, because of the low temperature during the winter. Garman (1917) has shown by experiments that a temperature of 0° F. for twenty-four hours will destroy all stages of this pest. Thus the insects are probably never able to live thru the cold winters in the bean fields. At a temperature of 50° F., feeding and reproduction are so checked that little harm results. A grower in New York who saves his seed from his crop of the preceding year and keeps it in a barn or some other cold place, need have little fear of weevil injury. The same is true where seed is kept in bean warehouses at low temperatures. In warm stores and seedhouses, however, which often have a few weevils present in left-over stock, the continuous multiplication of the pests often results in almost total destruction of the beans.

Fig. 99. The blue-banded millepede, × 2½

The Blue-Banded Millepede
(*Julus caeruleocinctus* Wood)

In July, 1917, a bean field near Batavia, New York, showed a heavy infestation of the millepede, or thousand-legged worm, *Julus caeruleocinctus* (of the order Diplopoda) (fig. 99). The soil in this field is sandy, and when observed by the writer it was dried out and crusted, altho only two weeks before it had been very wet. The millepedes were feeding on the plant parts below ground and had eaten the main roots to such an extent that some of the plants were almost severed from them (fig. 100, C). Nearly every plant

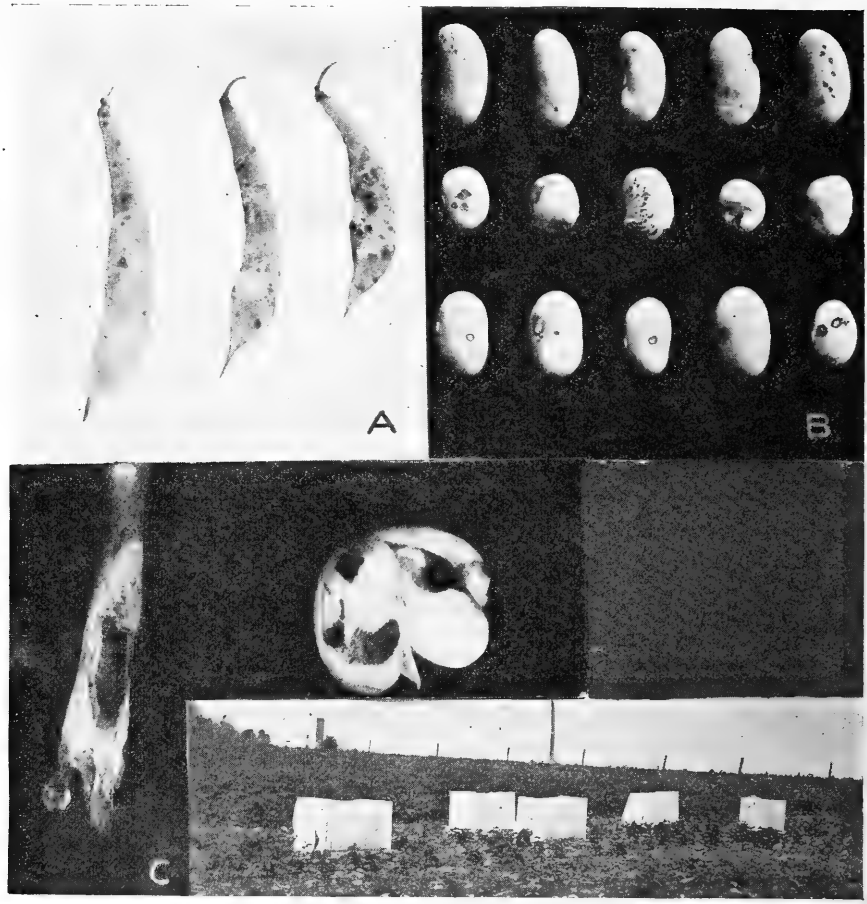

FIG. 100. SOME INJURIES TO BEANS

A, Bean pods punctured many times by *Adelphocorus rapidus*, reduced. B, Dimpled beans caused by punctures of sucking insects, and (bottom row) by a No. 2 insect pin with which they were pricked while still in the pod. C, Cavities made by the feeding of *Julus caeruleocinctus* on roots of beans, × 2. D, insect cages used in experiments in the transmission of bean blight

had been attacked, and frequently there were from five to ten of the pests around a single seedling. Reports of similar injury to beans were received from Orleans and Allegany counties.

J. caeruleocinctus shows a preference for decaying vegetable matter when this is present, but tender growing plants of fleshy texture may be eaten. In Lintner's early writings, records may be found of injury to geraniums,

melons, radishes, potatoes, and turnips. Lintner cites also an instance of injury to nursery stock which was planted after an infested crop of potatoes. The writer has observed these millepedes feeding beneath the ground on young hop vines before they had become hardened, and they have often been found in decaying roots and vines that had been injured by the hop-vine borer (*Gortyna immanis* Guenée). Millepedes thrive under moist conditions, and their attraction to growing plants is often due to decay started in the tissues by excess moisture.

The blue-banded millepede is said to deposit its small, white, spherical eggs in the spring, in clusters surrounded by particles of dirt and excreta. In midsummer, specimens of all sizes may be found feeding together. Two hundred millepedes were found in one potato by Lintner. The pests often gather and crawl over one another, forming moving balls of animal life. Late one evening in September, 1919, at Perry, hundreds were found crawling on sidewalks, in gutters, and even up the sides of houses. By morning they had nearly all disappeared.

There is no satisfactory control for millepedes under field conditions. A bait of poisoned potato buried in the ground is said to be of use in gardens. Tobacco dust seems to have some repellent effect, and on a small scale spraying the ground with Black-leaf-40, 1 part to 750 parts of water as recommended for control of the hothouse millepede (*Oxidus gracilis* Koch), may be effective.

THE SOLANUM ROOT LOUSE

(*Trifidaphis radicicola* Essig[9])

Each year a few bean plants have been found with their roots serving as hosts for the solanum root louse, *Trifidaphis radicicola* (Homoptera, Aphididae). If the aphides are numerous, the leaves turn yellow and the plants take on a wilted appearance, due to the injury to the lateral roots caused by the feeding of the pest. Infested plants have been found from June 22 to August 22. Only the apterous forms of the insect were seen, and usually there were more immature than fully developed lice present. These aphides are cream-colored, but their powdery covering frequently gives them a white, woolly appearance. An ant, *Solenopsis molesta* Say, is often in attendance.

A bean grower near Castile, New York, informed the writer that in 1915 his entire field was so badly attacked that the crop was ruined. When beans were planted in this field the next year they were again infested and had to be dragged up. Lice of this species have also been found in small numbers near Batavia, in Genesee County.

T. radicicola is reported from California by Essig (1909 and 1913) as feeding on rough pigweed (*Amaranthus retroflexus*), beet (*Beta vulgaris*), black nightshade (*Solanum nigrum*), and potato (*Solanum tuberosum*).

[9] Determined by Miss E. Patch.

It is probable that the insect may be found on weeds in New York and is injurious to beans only when they are planted after other infested hosts.

THE WHEAT WIREWORM
(*Agriotes mancus* Say)

Larvae of the wheat wireworm, *Agriotes mancus* (Coleoptera, Elateridae), may be found each year feeding in the roots of field beans near Perry, New York (Plate LXX, 4). This is especially noticeable when the plants are already weakened by the dry root-rot caused by *Fusarium martii phaseoli*. The taproot, part y destroyed by the disease, is a place of easy entrance for the larvae (fig. 96, D, page 1012), and when once inside they frequently eat their way upward as far as the first leaves. Several specimens may be found in a single plant, and if the root-rot also is present the plants often have a drooping, wilted appearance. It is usually impossible to absolutely distinguish the injury caused by the insect from that caused by the disease. Rarely have plants with healthy roots been found to contain wireworms.

Larvae of this species have also been found feeding in the roots of lamb's-quarters and of ragweed growing in bean fields. The life history of the insect covers a period of three years (Hyslop, 1916). Adults were taken by sweeping during May and June in 1919

As far as the writer has observed, serious injury from wireworms has been restricted to single plants, or, at most, to small parts of a field; and their presence may be explained by the practice of planting beans after sod, which is the normal host of the insect.

THE RED SPIDER
(*Tetranychus telarius* L.)

In a summer that is hot and dry, beans may suffer from the red spider, *Tetranychus telarius* (of the order Acariña) (Plate LXXI, 5). In 1918 the plants on the experimental field at Perry were covered with these pests; the leaves turned yellow and the growth was stunted. The total rainfall at Perry during July and August of that year was only 2.37 inches, whereas the normal for these two months is 6.05 inches. In 1919 the red spider was common in some parts of Genesee, Orleans, and Niagara Counties, where again the rainfall was below normal. It may be occasionally found on beans in any year, but when the growth of leaves is luxuriant the slight damage that it causes is easily overlooked. This mite has many native hosts, and fields that have weeds along the edges or between the rows usually show a heavier infestation.

Injury by *T. telarius* may be recognized by many small brown spots on the upper surface of the leaves, where the plant cells are killed. On the under surface of the leaves, small webs may be observed, and the small yellow, green, or red mites may be found crawling or feeding among

the strands of silk. Each brown area seen on a leaf represents the place of feeding of a mite below, and as these marks increase, the leaf becomes spotted, turns a sickly yellow, and in some cases drops. The lower leaves are attacked first, and as these are destroyed, the small creatures climb higher in search of new food.

WHITE GRUBS, OR MAY BEETLES
(*Phyllophaga* sp.)

White grubs, the larvae of May beetles (Coleoptera, Scarabaeidae), tho occasionally found, have not been reported as a serious pest of field beans in western New York during the past four years. In 1917 the beetles were present in very large numbers around electric lights at Perry. The writer had 184 specimens, collected between June 12 and June 25, identified by Mr. Henry Dietrich, who found 137 *Phyllophaga fusca* Froh. males and 38 *fusca* females, and 6 *P. anxia* (*dubia*) Leconte males and 3 *anxia* females. *P. fusca* is believed by Forbes (1916) to pass thru a three-years cycle. In 1920 a few beetles were collected around lights, but this brood was much smaller than the one observed in 1917. In rare cases the writer has found, in digging around a wilted bean plant, that a white grub had cut it off. Several plants of this type were found in 1919, and one beetle (*fusca*), bred from a grub found on July 3, changed to the adult stage on September 1. It would have emerged normally in the spring of 1920.

Injury from white grubs occurs usually when cultivated crops are planted after sod in a year following one in which there was a large emergence of parent beetles. The May beetles, according to Davis (1918), prefer to oviposit in fields of oats, barley, wheat, timothy, or sod, rather than in those where there are good catches of clover and alfalfa or where there are cultivated crops such as corn and beans. In western New York a common rotation is one of wheat, clover, and beans. If, in this New York rotation, the beetles are abundant during the year when a field is in wheat, there may be many small larvae present the next year; but, since the grubs do not seriously damage clover, the crop then growing, they might easily escape notice. As neither clover nor beans are attractive to the beetle for oviposition, it is evident that when this rotation is followed, little damage from the grubs should be experienced in western New York. Serious infestations of the grub occur only when pasture land or a crop of one of the small grains, such as barley, oats, or wheat, is followed the next year by beans.

THE ROSE CHAFER
(*Macrodactylus subspinosus* Fab.)

In the summer of 1917, beans in many parts of New York were damaged by the rose chafer, *Macrodactylus subspinosus* (Coleoptera, Scarabaeidae).

Reports of injury to the bean crop by this insect were received from Fulton, Lewis, Madison, Essex, and Warren Counties. The principal injury results from the active feeding of the long-legged, grayish brown, adult beetles, which have been reported as destroying as much as 40 per cent of the leaves. Injury from this pest in 1917 was reported between June 28 and August 2.

On grapes, a spray of arsenate of lead (4 pounds of paste to 50 gallons of water or bordeaux mixture, with the addition of 2 gallons of cheap molasses) is said to be the most effective method of control. This should control the insect on beans also. The spray must be applied thoroly as soon as the first beetles are seen, and repeated if rains wash off the first application. Every leaf should be covered, and as a new growth develops this also should be coated with the spray.

THE SOUTHERN CORN ROOTWORM
(*Diabrotica duodecimpunctata* Fab.)

The small, yellowish green beetle (Plate LXXI, 7) known in the South as the southern corn rootworm, *Diabrotica duodecimpunctata* (Coleoptera, Chrysomelidae), and sometimes called the twelve-spotted asparagus beetle, is occasionally present in small numbers on beans in New York. In 1917 it was reported to be causing some injury to the leaves. The parent insect is a general feeder and may be found on many cultivated crops as well as on weeds that occur in and around fields and gardens.

In the South the larvae feed underground on corn and cause immense losses by killing the developing bud. The insects have been found attacking the roots of beans in New York, but there have been so few of them present that the damage to this crop has been negligible. The feeding of the parent beetle on the foliage may be controlled by a spray of arsenate of lead, 2 pounds of paste to 50 gallons of water.

THE BEAN LEAF BEETLE
(*Cerotoma trifurcata* Forster)

Each year a few specimens of the bean leaf beetle, *Cerotoma trifurcata* (Coleoptera, Chrysomelidae), have been found on beans in western New York, but they have not been present in sufficient numbers to cause appreciable damage. The parent beetle (Plate LXXI, 9) is about one-third of an inch in length, and is yellowish in color, with a black head and black markings on the wing covers.

The bean leaf beetle has been found on beans from July until the middle of September. It has been noticed also on ragweed and lamb's-quarters growing in bean fields, and on carrot tops near by. Bush clover, hog peanuts, and beggarweed are likewise reported as hosts. At rare intervals the insect appears in parts of this and other States, destroying field and garden beans, soybeans, and cowpeas by feeding on the leaves.

When control measures are necessary, a spray of arsenate of lead, 2 pounds of paste to 50 gallons of water, applied when the beetles first appear, will suffice.

THE APPLE LEAF HOPPER
(*Empoasca mali* LeB.[10])

The apple leaf hopper, *Empoasca mali* (Hemiptera, Cicadellidae (Plate LXXI, 4), has at times been found in small numbers on field beans at Perry, but the insects have not been connected with any deformation of the plant. In some parts of the State, particularly near Lake Ontario, where pea beans are grown, this insect has been more plentiful, and it has seemed probable that bean mosaic, a destructive disease of pea beans, may be transmitted by this pest. This disease, however, which may be recognized by a curling of the leaves and the appearance of mottled light-and-dark areas on the foliage, has been known to occur and spread when leaf hoppers were not present.

Dr. Robert Matheson, working in conjunction with Dr. Donald Reddick, of the Department of Botany at Cornell University, found that he could produce a curling of the leaves of pea bean plants when leaf hoppers transferred from infested beans were caged over healthy plants. These plants later outgrew the curling, however, and mosaic did not develop, and so the experimental evidence would tend to show that the disease is not carried by *E. mali*. Further tests must be made before a definite statement can be given.

GRASSHOPPERS
(*Melanoplus atlantis* Riley, M. *femur-rubrum* DeGeer, and *M. bivittatus* Say)

Bean fields with a border of grass and weeds, or adjoining meadows or pastures, are often attacked by grasshoppers. Nearly every year a few poorly-cared-for fields have shown some injury. Three specimens of grasshoppers have been mainly blamable for the work — *Melanoplus atlantis*, *M. femur-rubrum*, and *M. bivittatus* (Orthoptera, Acrididae). The eggs of the insects have often been found in fence corners or in the sod border of fields, and many newly hatched nymphs have been taken in these places during May and June. The beans near the edges of fields usually suffer the most; in fact, it is not unusual to find the plants of the first few rows riddled by the pests, while the central part of the field is unharmed.

INJURIES TO BEANS IN THE POD, CAUSED BY HEMIPTEROUS INSECTS
(*Adelphocorus rapidus* Say, *Euschistus variolarius* Palisot de Beauvois, *Lygus pratensis* L.)

During the past four years the Cornell University Agricultural Experiment Station has received many samples of beans showing deformations

[10] Determined by E. D. Ball.

which varied from circular depressed areas, each with a dark spot in the center, to ragged holes, with the bean coat badly ruptured (Plate LXXI, 2, and fig. 100, B). The term *dimples* has been applied to these scars.

Since these markings bear a strong resemblance to hemipterous punctures on other plants, specimens of the dusky plant bug, *Adelphocorus rapidus* (fig. 101), one of the commonest mirids in western New York bean fields, were caged over a potted bean plant on August 15, 1918. When examined on September 4, the pods on this plant were misshapen and covered with dark, raised, wart-like areas (fig. 100, A). The seed in these pods showed evidence of dimpling.

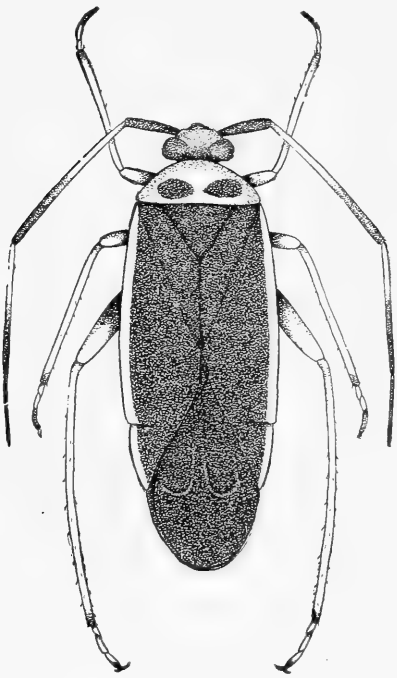

Fig. 101. The dusky plant bug, Adelphocorus rapidus

(Reproduced by courtesy of the Iowa College Agricultural Experiment Station)

In the summer of 1919 an effort was made to verify this observation and to find other insects that might have a share in the work. On August 11 a cage containing *A. rapidus* was placed over two bean plants, the pods of which were still green. When these were examined on August 28, most of the beans were dimpled. One hundred pods picked near the cage contained only one dimpled seed.

The feeding of *A. rapidus* frequently produces such ragged, discolored marks on the bean seed that it would seem that the insect, in addition to removing juices from the bean, possibly secretes a toxin that acts on the bean tissues. The nature of the puncture appears to be influenced by the stage of development of the pod at the time of the attack. The seed is stunted when punctured, and the subsequent growth about the injured part produces the dimple. Beans the pods of which are still green tho nearly mature, tend to suffer the most. In addition to feeding on the pods, the insect attacks also the blossoms, the leaves, and the stalks, but on these no serious deformation seems to result.

It is not always easy to distinguish, by their outward appearance, the pods that contain dimpled beans. The pods may be free from the roughened brown areas and still contain injured beans. Some have been found

on which only a dark green spot on the lighter green of the pod gave evidence of the deformation within.

Other insects that produce pits in beans are the spined tobacco bug (*Euschistus variolarius*, Plate LXXI, 1), of the family Pentatomidae, and the tarnished plant bug (*Lygus pratensis*). Specimens of *Euschistus variolarius* placed with beans on August 19 had produced small pits on them by September 8. Nymphs and adults of *Lygus pratensis* left with a plant for nineteen days also produced small dimples. Similar work of this insect was reported from Michigan some years ago. During late summer both these insects, together with the apple leaf hopper (*Empoasca mali*), have been found in the field with their beaks inserted in the pods. Cage experiments seem to show, however, that the beak of the leaf hopper is too short to penetrate the pod and injure the beans within. In the summer of 1920, these experiments were repeated and the injuries from the insects were of the same kind as had been caused by them the preceding year.

The extent of the damage caused by these pests is not great, but each year there are a few beans of this kind in the product of almost all fields and gardens. Injury is especially noticeable in places where ragweed and lamb's-quarters are allowed to grow. The most disfigured of the field beans are discarded, with the diseased and immature seed, when they are picked and graded in the warehouse.

The Rôle of Insects in the Transmission of Bean Diseases

Bean diseases frequently spread thru a field with great rapidity, and it sometimes appears as tho this spread might be due to, or at least hastened by, the presence of insects. In cooperation with Dr. W. H. Burkholder, of the Department of Plant Pathology at Cornell University, experiments were conducted in the summer of 1918 in an effort to determine what insects were instrumental in the spread of the bacterial blight of beans (caused by *Bacterium phaseoli* E. F. Smith).

On August 22, 1918, eight specimens of each of the commoner insects on bean foliage, including the red-headed flea beetle (*Systena frontalis*), the dusky plant bug (*Adelphocorus rapidus*), the apple leaf hopper (*Empoasca mali*), and the nine-spotted lady bug (*Coccinella novemnotata*), were rubbed in a virulent culture of the blight organism or allowed to crawl for an hour on bean leaves smeared with the culture. The insects were then placed in separate field cages (fig. 100, D, page 1016) on varieties of beans free from blight but susceptible to it. As a check, insects of the same species, collected in the same field but not treated with the pathogene, were placed in similar cages. Blight did not develop in any of the cages.

In 1919 the same species of insects that were used in 1918, and in addition the tarnished plant bug (*Lygus pratensis*), were used in the experiments. The insects were taken from a severely blighted field of red kidney beans, and after being caged for some time with these diseased plants they were

placed in field cages with beans free from the disease. Blight did not appear in any of the cages.

In examining bean seed punctured by *Adelphocorus rapidus*, Dr. Burkholder has found undetermined bacteria present in large numbers. It would seem, therefore, that this common sucking insect might be capable of transmitting the organism that causes bean blight, but most of the evidence thus far obtained is negative.

It is unusual to find *A. rapidus* present in sufficient numbers to be the sole agent in the spread of blight. The writer still feels that the commoner *Lygus pratensis* may sometimes carry the disease as it migrates from plant to plant in search of food, and further experiments should be carried on with *Empoasca mali* before it is safe to say that this species is not partially blamable for the spread of the blight organism. Plant lice have been found but rarely on beans in New York, and never in quantities that would justify placing much blame on them.

Dr. Robert Matheson, working in conjunction with Dr. Donald Reddick, of the Department of Botany at Cornell University, found that he could transfer bean mosaic, the causal organism of which has not been isolated, from one bean plant to another by means of an undetermined plant louse, but that *Empoasca mali*, *Lygus pratensis*, *Systena hudsonius*, *Systena frontalis*, *Epitrix cucumeris*, and *Tetranychus telarius*, seemed unable to transmit the disease.

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(*Agriotes mancus*)

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(*Tetranychus telarius*)

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(*Phyllophaga* sp.)

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(*Diabrotica duodecimpunctata*)

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(*Cerotoma trifurcata*)

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(*Melanoplus atlantis, M. femur-rubrum M. bivittatus*)

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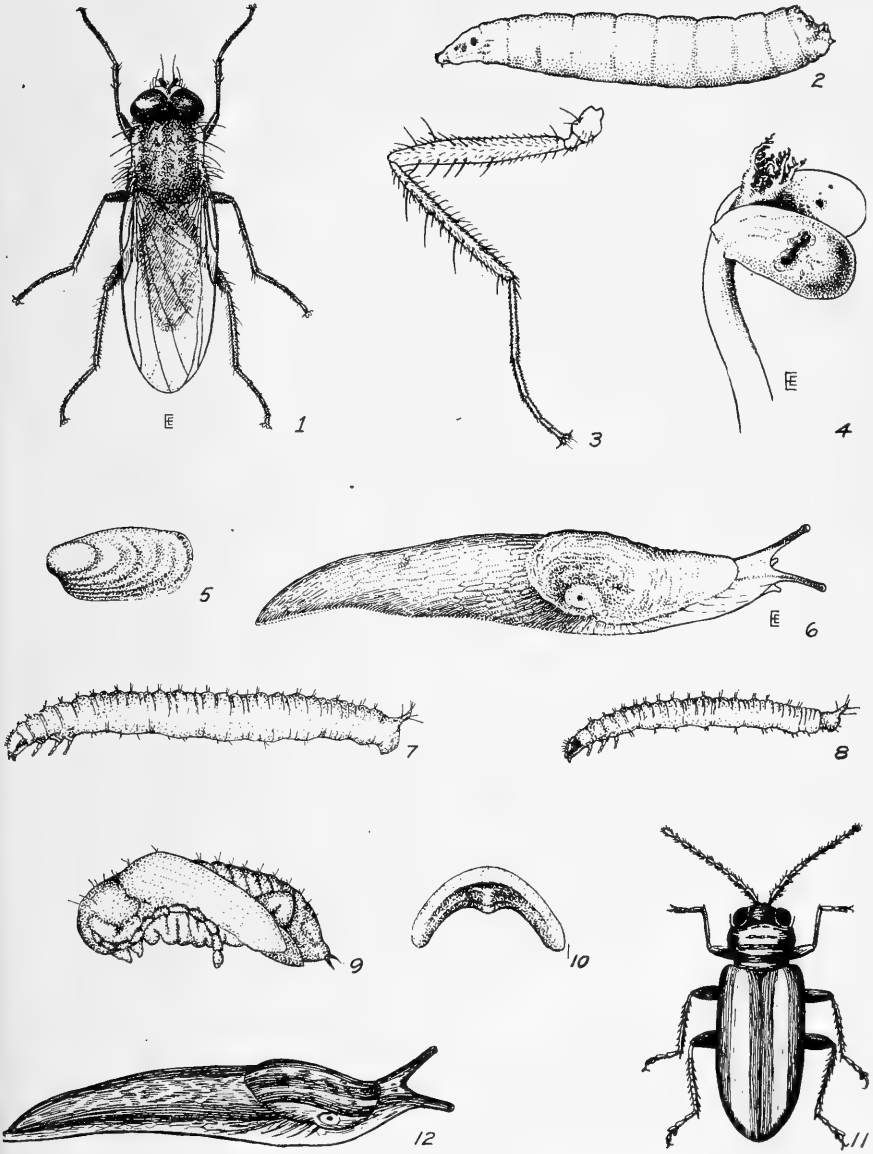
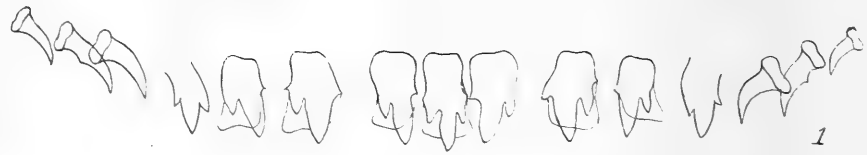
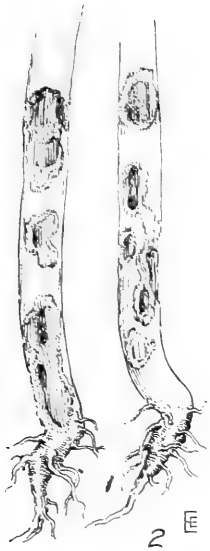
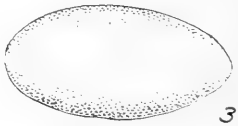


HYLEMYIA CILICRURA, AGRIOLIMAX AGRESTIS, ARION CIRCUMSCRIPTUS, SYSTENA TAENIATA, AND SYSTENA FRONTALIS

Hylemyia cilicrura: 1, Parent fly, with wings in normal overlapping position, × 8. 2, Larva, or maggot, × 8. 3, Third leg of male, showing the row of regular bristles on the tibia, × 18. 4, Injury to the plumule and cotyledons of a bean seedling, caused by the larva of *H. cilicrura*, × 1½
Agriolimax agrestis: 5, The shell. 6, The slug. 10, The jaw of *A. agrestis.* (All redrawn after Taylor)
Arion circumscriptus: 12, A common imported slug, *Arion circumscriptus*, × 2
Systena taeniata: 8, The larva, × 9. 9, The pupa, × 9. 11, The adult beetle, × 8
Systena frontalis: 7, The larva, × 9

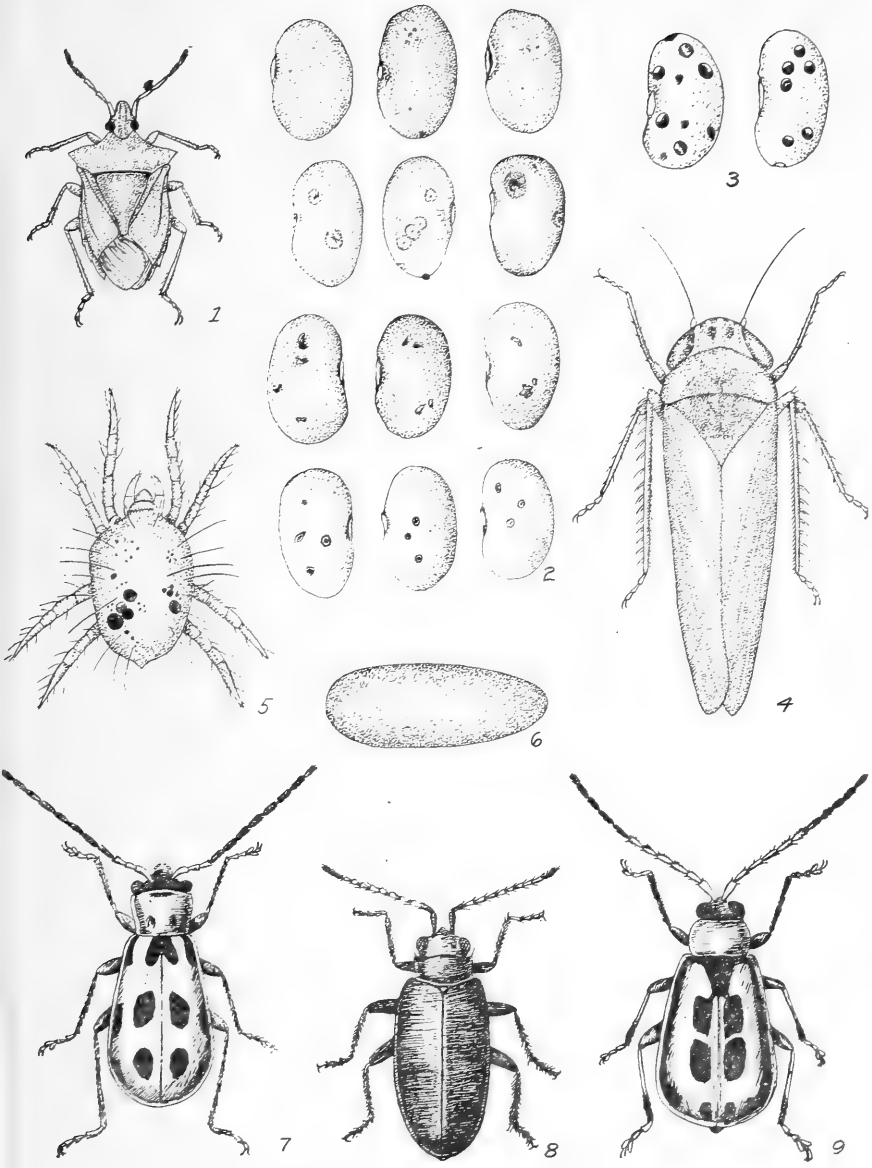






STAGES OF VARIOUS SPECIES, AND SOME RESULTS OF THEIR WORK

1, Types of teeth found in the radula of *Agriolimax agrestis* (redrawn after Taylor). 2, Stems of young bean plants showing the result of feeding by *A. agrestis*
3, Egg of *Systena taeniata*, × 48
4, Larva of *Agriotes mancus*, × about 4
5, Feeding holes made by *Plathypena scabra* on small bean pods
6, The spotted garden slug, *Limax maximus*, slightly reduced



STAGES OF VARIOUS SPECIES, AND SOME RESULTS OF THEIR WORK

1, The spined tobacco bug, *Euschistus variolarius*, × 2
2, Beans punctured by sucking insects, causing marks known as *dimples*: top row, dimples caused by *Euschistus variolarius*; second row, by *Adelphocorus rapidus*; third row, by *Lygus pratensis*; bottom row, marks made by a No. 0 insect pin
3, Beans showing the exit holes of the bean weevil, *Acanthoscelides obtectus*
4, The apple leaf hopper, *Empoasca mali*, × 17½
5, The red spider, *Tetranychus telarius*, × 6
6, Egg of *Systena frontalis*, × 40; 8, adult, × 7
7, Parent beetle of *Diabrotica duodecimpunctata*, × 5
9, The bean leaf beetle, *Cerotoma trifurcata*, × 3½

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CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

THE INSECT FAUNA OF THE GENUS CRATAEGUS

WALTER H. WELLHOUSE

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CONTENTS

THE INSECT FAUNA OF THE GENUS CRATAEGUS

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WALTER H. WELLHOUSE

This paper is submitted as a result of three years of study of the insects that feed on the plants belonging to the genus Crataegus. The writer's object at the time when the work was undertaken was primarily to learn, by collecting and rearing, what insects occur on the trees of this genus in central New York. As the interest in the work increased, it was decided to widen the field and make the list more complete by including the insects that other workers have found to be eaters of Crataegus.

There are three older lists of insects feeding on Crataegus which have been helpful in the preparation of the present catalog. Kaltenbach (1872) [1] gives a list of 104 European species, Packard (1890) gives 46 American species, and Felt (1906) gives 28 American species. With the exception of these three lists, the material included in this paper is gathered from widely scattered references and from the writer's observations. Since food-plant indices are very commonly omitted from entomological writings, it is difficult to get a list of all the insects that feed on a plant. Such a list can be obtained only by scanning the pages of a multitude of papers containing biological notes on all orders of insects. Much of that kind of work has been done in the preparation of this catalog, but, since it has not been possible to see all papers that might contain accounts of insects feeding on Crataegus, the writer does not claim that his list is complete.

The catalog contains 382 species, representing 9 orders and 55 families. They are distributed as follows:

Acarina, 10 species:	
Eriophyidae	7
Phyllocoptidae	1
Tetranychidae	2
Orthoptera, 4 species:	
Gryllidae	1
Acridiidae	3
Odonata, 1 species:	
Agrionidae	1
Hemiptera (including Homoptera), 84 species:	
Miridae (Capsidae)	12
Tingitidae	4
Membracidae	4
Cicadellidae (Jassidae)	18
Psyllidae (Chermidae)	7
Aphididae	22
Coccidae	17
Thysanoptera, 1 species:	
Thrypidae	1
Coleoptera, 74 species:	
Elateridae	3
Buprestidae	6
Scarabaeidae	4
Cerambycidae	5
Chrysomelidae	12
Curculionidae	40
Ipidae (Scolytidae)	2
Anthribidae	1
Dermestidae	1
Lepidoptera, 184 species:	
Papilionidae	2
Nymphalidae	2
Pieridae	1
Lycaenidae	3
Sphingidae	3

[1] Dates in parenthesis refer to *Literature Cited*, page 1083.

Lepidoptera (*continued*):	
Saturniidae	3
Arctiidae	3
Noctuidae	27
Notodontidae	6
Lymantriidae	7
Lasiocampidae	10
Geometridae	27
Drepanidae	1
Nolidae	1
Psychidae	1
Limacodidae	1
Cossidae	1
Sesiidae (Aegeriidae)	3
Pyralidae	3
Tortricidae	30
Lepidoptera (*continued*):	
Yponomeutidae	7
Gelechiidae	6
Elachistidae	5
Gracilariidae	12
Glyphipterygidae	2
Nepticulidae	11
Cosmopterygidae	2
Lyonetiidae	4
Diptera, 16 species:	
Cecidomyiidae (Itonididae)	15
Trypetidae	1
Hymenoptera, 8 species:	
Tenthredinidae	7
Chalcididae	1

The catalog includes insects that have been taken on the Crataegus trees in five continents. The number of species reported from each continent is as follows: North America, 213 species; Europe, 203; Asia, 88; Africa, 11; Australia, 8. All but 45 of the North American species are believed to be distinct from those of the Old World. A single Australian species is distinct from those of other continents. The insects recorded from Asia and Africa are found also in Europe.

It will be noticed that the mites, which have similar habits, are included with the insects in this paper.

Some helpful references to entomological notes concerning each species have been included in the catalog, which is intended as an aid to other workers who are investigating the insects of our deciduous fruit trees and related plants.

Grateful acknowledgment is made to Professors Glenn W. Herrick and James G. Needham, of the Department of Entomology at Cornell University, under whose direction the work was done and whose kindly criticisms and suggestions are appreciated; also to Dr. W. T. M. Forbes, Dr. Edith M. Patch, Chas. W. Leng, Dr. P. B. Lawson, Professor Z. P. Metcalf, Dr. H. H. Knight, Professor Carl J. Drake, Dr. E. P. Felt, and Henry Dietrich, who have kindly aided in the determination of species; to Dr. K. M. Wiegand, who has kindly aided in the determination of species of Crataegus; and to Miss Lela G. Gross for able editorial assistance.

THE GENUS CRATAEGUS

Crataegus is the name of a group of trees and shrubs commonly known by their sharp thorns, white flowers (pink or red in a few cultivated varieties) in May, and red or yellowish fruit like minature apples in autumn. It is an ancient Greek name derived from *kratos* (strength), and was applied to the plants of this genus because of the hardness and durability of the wood.

Among the popular names by which the genus is known most commonly are the following: hawthorn, thorn apple, red haw, white thorn, and thorn, in America; hawthorn and may, in England; aubepine, in France (snellier, by French Canadians); Weissdorn, in Germany; spinalba, in Italy. As the name *hawthorn* seems to be the one most commonly used by English-speaking peoples, the writer has used it in this paper to represent all species of Crataegus.

The genus is placed by many botanists in the family Rosaceae. Other botanists have divided the Rosaceae group and formed an apple family, Malaceae, in which Crataegus is included along with Malus, Pyrus, Cydonia, Mespilus, Sorbus, Amelanchier, Aronia, and Eriobotrya.

The determination of species of Crataegus is as great a taxonomic problem to botanists as the determination of the parasitic Hymenoptera is to entomologists. During the first ten years of this century about one thousand species of Crataegus were described in North America. Many of them are now regarded as hybrids and varieties, and a still further reduction of species is in progress. This taxonomic uncertainty makes it impossible in many cases to recognize specific hosts for the insects that feed on the hawthorns.

Crataegus is distributed over most of the temperate parts of the Northern Hemisphere. The genus is not indigenous in the Southern Hemisphere except in America, where it follows the unbroken mountain chain through the Tropics and grows in the Andes Mountains. It is found as far north as Newfoundland, Norway, and Sweden, and extends southward to the Mediterranean borders of Africa and Asia Minor. The European species have been introduced into Australia and other European colonies in the Southern Hemisphere for cultivation.

Most species of hawthorns seem to thrive in any well-drained soil which is not acid and where rainfall is sufficient for the growth of forest trees, while a few species thrive in acid soils also. They are usually long-lived trees, and individuals one hundred years old are not uncommon.

Distribution is effected largely by means of birds and mammals, which eat the ripe fruits and carry the seeds in their digestive tracts to other communities. Within the same community, thickets are commonly formed from the new stems which grow from the roots of a single tree. Wherever the roots become exposed to light, as by washing on hillsides, a new stem may grow and a tree be formed from it.

ECOLOGICAL SUMMARY

The ecological relations of the hawthorns to their insect fauna may be summarized in a general way very briefly. The two basic needs of an insect which it is possible for a host plant to supply are food and shelter. The hawthorns furnish both food and shelter.

They furnish food for nearly all of the insects studied. A few exceptions, such as the snowy tree cricket (*Oecanthus niveus*) and the damsel fly *Lestes viridis*, procure their food elsewhere and use the hawthorn branches merely to shelter their eggs from the weather and their enemies. Every part of the tree furnishes food for some species of insect, as may be seen from the following outline:

Trunk and branches	40 species
A. External feeders (scales, aphids, and others), 19	
B. Internal feeders (borers), 21	
Roots (aphids)	1
Thorns (weevils)	1
Leaves	292
A. External feeders (miscellaneous), 235	
B. Miners (tineids, weevils, sawflies), 37	
C. Gall makers (aphids, mites, cecidomyiids), 20	
Flowers (thrips, maggots, caterpillars, beetles, and others)	12
Fruit (caterpillars, bugs, maggots, grubs)	30

The other basic need of insects which a host plant may supply is shelter. Most of the insects included in this paper are sheltered to some extent by the hawthorn, although the completeness of the shelter varies with the habits of each species of insect. Some are protected only by their position on the surface of the tree. Others are partially sheltered in rolled leaves, bark crevices, and the like. Still others are securely housed within the plant tissues. The degree of shelter secured by those species living externally on the surface of the plant varies so greatly and so gradually that no distinct lines of division can be drawn in so general a statement as this. The more distinct groups of internal feeders (borers, leaf miners, and gall makers) are indicated above and are distinguished from the external feeders, which receive less complete shelter.

The fact that so many species of insects feed at the expense of the hawthorns suggests the idea that these trees are in danger of extinction. Such is not the case, however, for the hawthorns when not weakened by drought or flood are very hardy, long-lived trees. Some indications as to why they so successfully withstand the feeding of the insects may be seen from a study of the following data, which are based on statistics given in the last sections of this paper:

APPROXIMATE FEEDING PERIOD OF HAWTHORN INSECTS

	Species		Species
March	11	August	117
April	54	September	124
May	190	October	80
June	232	November	23
July	131	Time of feeding unknown	58

FOOD PLANTS OF HAWTHORN INSECTS

Food plants restricted to Crataegus	57 species
Food plants including other related or associated groups	325 species

It will be noticed that there is a direct correspondence between the time of feeding of the insects and the time of growth of the trees. The greatest number of species feed during May and June, when the trees make their greatest growth. The number decreases slightly during July and August, at the time when droughts frequently check tree growth, and then it increases slightly in September, at the time when fall rains often cause a new growth. This relationship between the period of growth and the time of feeding seems to be one of Nature's adjustments for maint ining balance.

. The fact that a large majority of the insects feed on other host plants also, lessens the danger of destruction of the hawthorns and is another of Nature's provisions for maintaining balance. There are, of course, many other factors that tend to lessen the insect injury to the trees, such as the interrelations of the insects with their parasites and preyers, but so little is known about them that the writer makes no attempt to discuss them.

A host of bees, flies, and beetles visit the blossoms in quest of pollen and nectar. The winter buds in some species of hawthorn become coated with a sticky exudation, which attracts insects emerging in late winter, such as the stone flies and the chironomids. These transient members of the Crataegus fauna have been omitted from consideration in this paper. A list of insects that visit the blossoms is given by Knuth (1908).

In the preparation of the catalog of hawthorn insects it became noticeable that some of the species which have more than one host plant have chosen only closely related hosts, such as the apple, the pear, or the medlar, while many others have chosen their hosts from plants that grow in the same communities regardless of close botanical relationship. A study of these combinations of hosts and the habitats in which they grow has led the writer to believe that the hawthorns are members of at least five different plant communities, which may be described as follows:

1. Open woods. In woodlands where the growth habit of the taller trees permits sunlight to reach the ground so that an undergrowth may develop, such as that in a forest of oak, hickory, and elm, Crataegus is commonly found along with Corylus, Rhamnus, Carpinus, *Prunus spinosa*, and the like.

2. Deforested areas. Where a shrubby growth has sprung up after the destruction of a forest, numerous thorny forms such as Crataegus, Rubus, Berberis, and *Prunus spinosa* are frequently found.

3. Grazing lands. Hillsides or valleys where the soil is uncultivated and cattle are pastured are frequently dotted with Crataegus, Rosa, and crab apple, which because of their thorns can continue to thrive and outgrow the danger of being eaten by the cattle.

4. Stream banks. Just back of the willows and alders on moist alluvial soil beside streams, Crataegus grows to its greatest size and is associated with birch, willow, alder, and poplar.

5. Fence rows. Where shrubs are allowed to grow up along the fences, *Prunus virginiana*, Crataegus, wild plum, and wild cherry are frequently found closely associated.

In each of these five communities insects will be found which feed on the various plants of the community. For example, *Fsylla mali* Schmid.

feeds on Crataegus, Malus, Sorbus, Quercus, Ulmus, and Corylus, which may all be found in the open-woods community, as may the host plants of the flat-headed apple-tree borer, *Chrysobothris femorata* Fabr. On the other hand, the leaf beetle, *Cryptocephalus bipunctatus* Linn., feeds near the streams on such plants as Salix, Betula, Crataegus, and Corylus, and *Agrilus vittaticollis* Rand. is found along the fence rows on Crataegus, *Prunus virginiana*, and Amelanchier. No very distinct lines can be drawn between the members of these communities, since many of the plants and insects belong to more than one community.

THE RELATION OF CRATAEGUS INSECTS TO APPLE, PEAR, AND QUINCE

A more complete knowledge of the insects that feed on Crataegus is of considerable importance as an aid in the control of insect pests of the cultivated commercial fruits. It has for many years, since the days of Walsh and Riley, been recognized by entomologists as the original native host plant of a number of important insect pests which now attack the apple, the pear, and the quince in the northeastern section of the United States. In all probability new pests must be expected to attack the cultivated fruits in the future as the population of the country increases, since as a consequence less uncultivated land will remain where the insects may feed undisturbed on their natural hosts.

The main commercial fruits of the United States, such as the apple, the pear, the quince, and the cherry, are natives of the Old World and have been imported by man into America. With them were imported a number of foreign insects, such as the codling moth, the bud moth, and the sinuate pear borer, which continued to feed on them in this country. Many of the pests now destructive to these fruits, however, are native to North America and are not found in the Old World. Before the extensive planting of the imported fruits these insects must have fed on native plants. Among the most numerous of the native plants which are similar to the apple, the pear, and the quince are those of the genus Crataegus, and the members of this genus are widely distributed throughout many of our commercial fruit districts.

A young orchard which is set in the midst of hawthorns may be ruined in a few years by the insects that migrate to it from the surrounding trees. Well-established orchards may suffer from the attacks of new pests whenever there is a failure of the crop of wild haws or a clearing of the land occupied by hawthorns so that their natural guests must seek other hosts.

It is commonly known among entomologists that the apple maggot, *Rhagoletis pomonella*, was originally a hawthorn insect and that after the apple had been cultivated in North America for many years this insect selected the larger, juicier fruit of the apple for its home. It is still found in the haws but is now known as an apple pest.

The apple redbug, *Heterocordylus malinus*, is another hawthorn insect which has adopted the apple. It was formerly believed that the false apple redbug, *Lygidea mendax*, was also originally a hawthorn insect, but the observations of Cushman (1916), as well as those of the writer, indicate that *L. mendax* is a wild-crab insect and does not feed extensively on hawthorns.

The quince curculio, *Conotrachelus crataegi*, is a very common feeder in haws which has occasionally injured quinces seriously and has thus gained its common name. Likewise the lesser apple worm, *Laspeyresia prunivora*, has gained its common name because of occasional migrations from hawthorn to apple.

Baker (1915:10) considers the woolly apple aphis, *Eriosoma lanigera*, to have been originally an elm-Crataegus feeder which has adopted the apple and traveled around the world with it. The woolly aphis is undoubtedly common on hawthorns.

Numerous other native American insects that feed on apple, pear, or quince are included in the catalog of hawthorn feeders beginning on page 1090.

The possibility that foreign hawthorn insects may be imported and become pests in North America should also be considered. When introduced into a new environment away from their natural checks, these may become more important here. Recent examples of this are three small moths imported from Europe — the apple and thorn leaf skeletonizer, *Simaethis pariana*; the hawthorn ermine moth, *Yponomeuta padellus*; and the lesser bud moth, *Recurvaria nanella*. These have attracted the attention of economic entomologists in North America as apple and cherry pests, while in Europe they feed commonly on hawthorns.

Since the catalog of hawthorn insects included in this memoir lists their food plants and the continents where each species occurs, further examples of foreign hawthorn insects that are now in North America may be found there.

BIOLOGICAL NOTES ON INSECTS FEEDING ON CRATAEGUS, AS OBSERVED BY THE WRITER FROM 1917 TO 1920 [2]

ACARINA

Tetranychidae

telarius Linn., *Tetranychus* (Red spider)

The leaves of all species of Crataegus observed showed attack by *Tetranychus telarius*. The European hawthorns, however, seem to be more often severely injured by these mites than the native species. The

[2] The insects are grouped according to order and family, and arranged alphabetically by species within the family.

injury is severest in warm, dry periods. The leaves at first become grayish, due to the presence of a fine white web and the cast skins of the mites attached to them. Later they turn brown and their margins curl toward the surface on which the mites have fed. The adults hibernate among the fallen leaves and a few were found in bark crevices on the trunk in April. The tiny, round, white eggs are laid on the leaves. The mites breed continually on the leaves from June to October.

Eriophyidae

Eriophyes sp. No. 1 (Hawthorn serpentine gall of Jarvis)

The species of Eriophyes here described produces long, green or red, serpentine galls confined to the space between two of the larger veins and extending from the midrib toward the margin of the leaf (fig. 102). The

FIG. 102. LEAVES OF CRAETAEGUS PUNCTATA SHOWING SERPENTINE GALLS PRODUCED BY ERIOPHYES SP. NO. 1

gall consists of a wavy projection on the upper side of the leaf and a wavy incision on the lower side. In cross section the leaf appears convoluted, with the galls projecting upward as loops or pockets in which the mites

live (fig. 103). The leaf does not become thickened in these galls. The galls become extremely abundant on some trees, so that almost every leaf is deformed. The mites seem to prefer the shady branches of trees, rather than those in bright sunlight. They become most abundant during August, when the galls are swarming with the microscopic white mites. The galls were found most abundantly on *Crataegus punctata*, but they were found also on *C. pruinosa* and other native hawthorns.

FIG. 103. CROSS SECTION OF A CRATAEGUS LEAF, THROUGH THREE SERPENTINE GALLS

FIG. 104. HAWTHORN MARGINAL GALLS

Eriophyes sp. No. 2 (Hawthorn marginal gall)

Galls very similar to those of *Eriophyes goniothorax* Nal., which are found on hawthorns in Europe, are produced by *Eriophyes* sp. No. 2. The margin of the leaf is curled tightly downward for a distance of two centimeters or more (figs. 104 and 105), and the curled margin is paler green than the rest of the leaf. The mites live within the curl. This gall is not very common about Ithaca, but was found in a few cases on *Crataegus coccinea*.

Eriophyes sp. No. 3 (Thorn leaf pouch gall)

Many small, pale green pouches, standing on the upper side of the leaf and opening beneath the leaf by a small slit, are caused by microscopic white mites which live within the pouches. The galls vary in size and shape, but are generally about two millimeters high and are rounded on top (figs. 106 and 107). They may be found at any place on the leaf except on the larger veins. They are fairly common on *Crataegus punctata* but are not so abundant as the serpentine galls.

FIG. 105. CROSS SECTION THROUGH CURLED EDGE OF LEAF

FIG. 106. THORN LEAF POUCH GALLS

ORTHOPTERA

Acridiidae

atlanis Riley, *Melanoplus*
bivittatus Say, *M.*
femur-rubrum De Geer, *M.*

The common grasshoppers *Melanoplus atlanis*, *M. bivittatus*, and *M. femur-rubrum* sometimes leave their herbaceous host plants to feed on the foliage of the lower branches of hawthorn trees. The older nymphs and adults have been observed feeding in August and September. They feed irregularly on the leaves, sometimes eating the entire leaf and sometimes eating only the apex or one side of it.

HEMIPTERA

Miridae (Capsidae)

communis Knight, *Lygus*

One adult of *Lygus communis* was taken on June 21 and four were taken on August 2, puncturing the leaves of *Crataegus punctata*.

dislocatus Say, *Horcias*

A few adults of *Horcias dislocatus* were found feeding on leaves of *Crataegus punctata* in June. They are black, rather stout, and 6 millimeters long.

malinus Reuter, *Heterocordylus*
(Dark apple redbug)

Nymphs and adults of *Heterocordylus malinus* are very common on native hawthorns, where their red color and rapid running over the branches make them very conspicuous. The young nymphs begin to appear about April 15, when

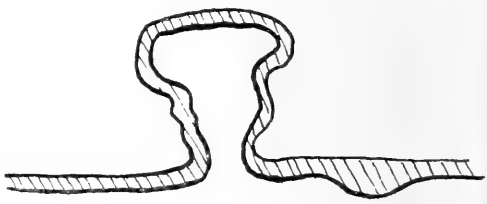


FIG. 107. CROSS SECTION THROUGH A THORN LEAF POUCH GALL

the blossom clusters have just begun to separate and before the blossoms show pink. They puncture the leaves and the tender twigs but do not cause any noticeable injury. After the fruit sets they feed on the fruit also and cause very slight dimples where they puncture it. They become adult in late May and early June, and begin ovipositing in the twigs about June 15. The egg is deposited in a small slit made with the beak at the base of a young twig. Adults were found on the trees until late July.

mendax Reuter, *Lygidea* (Bright apple redbug)

A few nymphs of *Lygidea mendax* were found feeding on the leaves and fruit of Crataegus in late April and in May. They are not so common as *Heterocordylus malinus*. In the warm laboratory the eggs hatched on March 27 on *Crataegus punctata* twigs, but no nymphs were found in the field until the blossoms were opening on April 25. Adults were found from June 2 to August 14. One adult in a breeding cage oviposited on June 19 in a twig of *Crataegus crus-galli*. She chose a year-old twig, drilled a hole through the bark at the base of the twig, and then, turning about, thrust an egg into the cavity.

ornatus VanD., *Orthotylus*

A few adults of *Orthotylus ornatus* were found feeding on the leaves of *Crataegus pruinosa* in June. They are brownish, spotted, slender, and 5.5 millimeters long.

ostryae Knight, *Lygus*

A few adults of *Lygus ostryae* were taken puncturing the leaves of *Crataegus punctata* in late June. They are pale yellowish brown, and are otherwise similar in appearance to the tarnished plant bug.

pellucida Uhl., *Diaphnidia*

The pale green nymphs of *Diaphnidia pellucida* are rather numerous on the foliage of *Crataegus punctata* during late May and early June. They run rapidly over the branches when disturbed, and feed on the leaves and tender twigs. Adults appeared from June 10 to June 15 in rearing cages in the laboratory, and others were found in the field on June 18. They are delicate, slender, pale green, and about 4 millimeters long.

pratensis Linn., *Lygus*

Adults of *Lygus pratensis* which have lived through the winter are sometimes found puncturing the buds of Crataegus in April, as soon as the buds show green, and a few were found puncturing the young fruit in late May.

univittatus Knight, *Lygus*

Adults of *Lygus univittatus* are rather common during late May and June, puncturing the leaves and fruit of native hawthorns. They resemble *L. communis* very closely, but are generally paler.

Tingitidae

bellula Gibson, *Corythucha* (Plates LXXII and LXXIII)

Although the original description of *Corythucha bellula* was published but recently (Gibson, 1918), the species seems to be fairly common where its host plants occur, and it has probably been confused with *C. cydoniae* by earlier observers who must have seen it on the hawthorns. It has been found by Drake in Ohio and by Criddle in Manitoba.

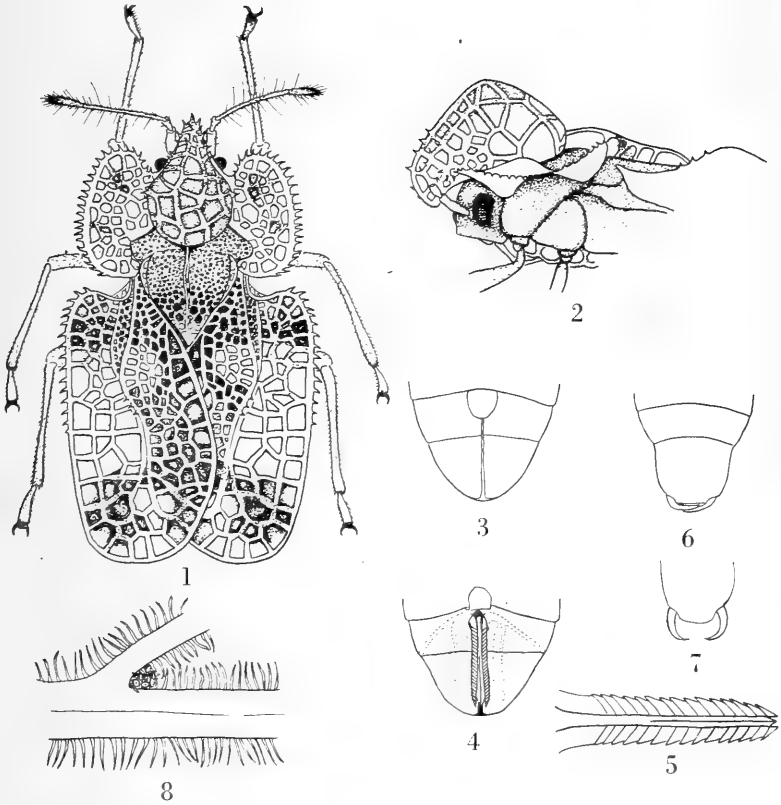
The host plants include those species of Crataegus that have hairy leaf veins, and also *Alnus incana* and *Ribes oxyacanthoides*. The writer has found the insect breeding in abundance on *Crataegus neofluvialis* and to some extent on *C. albicans* and *C. punctata*. The hawthorns with smooth leaves, such as *C. pruinosa*, *C. crus-galli*, and *C. oxyacantha*, even when their branches were intermingled with those of trees that were badly infested, revealed no nymphs nor eggs.

In a large thicket of *C. neofluvialis* trees near the Cornell University campus, the leaves were so discolored by the end of July that they attracted attention several hundred yards away. By the middle of August the leaves were falling, and the branches were bare by September 1. No fruit matured on these trees. A few scattered trees of this species in other directions from the city were also badly infested. Individual trees of *C. albicans* and *C. punctata* showed an occasional branch badly infested and with leaves discolored. The injury is caused by the nymphs and the adults puncturing the under surface of the leaf and sucking the sap, producing at first a mottled effect due to the pale areas around the feeding punctures, while later the leaf turns brown and falls to the ground. Ornamental plantings of Crataegus in parks and gardens are rendered unsightly and weakened by this injury.

There are two generations annually at Ithaca. The first brood hatches in July from eggs laid in late May and in June, and the nymphs become mature in from twenty to twenty-five days. The second-brood eggs are laid in late July and in August, and the adults appear in late August and in September.

The adults of the second brood hibernate among the fallen leaves and in crevices of the bark. Many of them remain on the leaves on which they were feeding before the leaves fell. They appeared the last of May, and during early June were feeding on the new Crataegus leaves. As a rule only one pair of adults was found on a leaf, and they remained feeding and ovipositing on that same leaf for several days. After emergence from the nymphal skin in September, the adults of the second brood continue feeding on the leaves until they fall, in late September or in October.

The egg is subelliptical, with the basal end rounded and the apical end bent slightly to one side and capped with a rather broad cylindrical collar



CORYTHUCHA BELLULA

1, Adult. 2, Lateral view of hood and carina. 3, Tip of abdomen of female, with ovipositor at rest. 4, Same with ovipositor exserted; chitinized parts within body shown by dotted lines. 5, Ovipositor. 6, Tip of abdomen of male, with claspers at rest. 7, Same with claspers exserted. 8, Eggs in position among hairs in axil of leaf veins

surmounted by a low cone with irregular ridges extending from base to apex. From the apex of this cone there arises in some cases a short, blunt prolongation, but often this is absent. The egg is without waxy covering over the chorion, which is smooth, unsculptured, and of a shining dark-brown color but somewhat lighter toward the base. The cap, or cone, is often whitish. The egg, exclusive of the apical prolongation of the cap, is 0.52 millimeter long, and 0.21 millimeter broad at its greatest width.

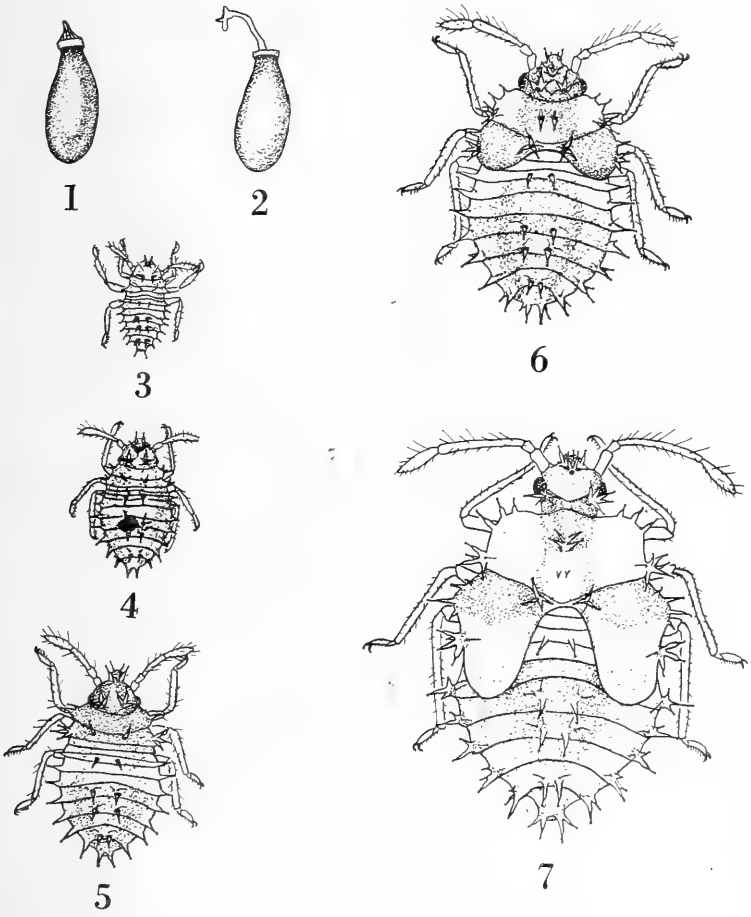
The eggs are laid on the under surface of the leaf, in the axils formed by the midrib and its lateral branches. Although the female has a well-developed, sawlike, four-valved ovipositor, the eggs are not inserted into the leaf tissue. They are placed among the hairs on the veins and are in some cases glued together with an adhesive material. They are generally laid in small groups, some groups containing as many as eighteen or twenty eggs; but occasionally they are laid singly. In counting the number of eggs on one hundred infested leaves the writer found an average of forty-nine eggs to a leaf. Occasionally a leaf had seventy-five or eighty eggs on it. The egg-laying period extends over several weeks, so that eggs, nymphs, and adults may be found at the same time in July and August.

Eggs laid on June 2 hatched on July 9 and 10, while the eggs of the second brood, laid on July 29 and 30, hatched on August 15 and 16. This indicates an incubation period of about thirty-seven days in the cooler temperature of June, and eighteen days in July and August when the average temperature was higher.

The conical egg cap is pushed up by the nymph as it begins to emerge from the egg still inclosed in the embryonic membranous sac. When about halfway out of the eggshell the nymph splits the membranous sac and slips it off over the head, leaving it with the egg cap on the outer end hanging out from the empty eggshell.

After emerging and drying, the nymphs begin to feed at once in colonies near the eggshells. They molt five times, feeding from three to six days between molts, the earlier stages requiring three or four days while the later ones require five or six days. In molting, the cuticula breaks along the median dorsal line from the front of the head to about the second abdominal segment. The insect on emerging is limp, and is almost colorless except for the eye facets which are bright red. The body color soon darkens and the eyes a few hours later become black. During the fifth stage the nymph wanders about more freely over the leaf and in some cases goes to adjoining leaves. Descriptions of the nymphal stages follow.

First stage.— Length 0.5 mm., greatest width 0.15 mm. General shape an elongate ellipse, somewhat broader cephalad than caudad and more elongate than in the later stages. At first almost colorless but soon becoming dark brown. Beak 4-segmented and extending back to sixth abdominal segment. Antenna 3-segmented, the basal two segments being shorter than the third segment; basal segment without spines or hairs, second segment with



YOUNG STAGES OF CORYTHUCHA BELLULA

1, Egg. 2, Egg after hatching. 3, First-stage nymph. 4, Second-stage nymph. 5, Third-stage nymph. 6, Fourth-stage nymph. 7, Fifth-stage nymph

a few short hairs, third segment with numerous long spines and hairs, some with rounded tip and conical base, others with pointed tip. Head with five prominent dorsal tubercles, two slightly separated just above base of beak, each bearing a round-tipped spine; one tubercle back of these on median line bearing two spines; two tubercles near posterior margin, widely separated and each bearing two spines. Pro- and mesothorax having lateral tubercles with a spine on each, and mesothorax having a pair of dorsal tubercles with one spine on each. Metathorax and first abdominal segment without spines. Legs armed with short, pointed hairs and two bent, sharp, terminal claws. Nine abdominal segments visible above, each of these except the first bearing on each lateral margin a tubercle surmounted by a round-tipped spine; two dorsal tubercles on second, fifth, sixth, and eighth abdominal segments, those on second and eighth segments bearing one round-tipped spine each, and those on fifth and sixth segments bearing two spines each; tenth abdominal segment visible from a lateral or ventral view, this segment bearing no spines nor hairs; minute awl-shaped spinules over dorsal surface, especially on large tubercles of fifth and sixth abdominal segments and on thorax. (Plate LXXIII, 3.)

Second stage.— Length 0.68 mm., greatest width 0.27 mm. Body broader in proportion to its length than in first stage; dark brown in color, with numerous minute spinules over dorsal surface, covering it much more completely than in first stage. Additional small spines on both dorsal and lateral tubercles, and the round-tipped spines present before having a slightly longer conical base in this stage. (Plate LXXIII, 4.)

Third stage.— Length 0.82 mm., greatest width 0.44 mm. Antenna with four segments. Round-tipped spines arising from a base longer than the spines, and a few additional small spines on tubercles. Pro- and mesothorax beginning to increase in prominence. (Plate LXXIII, 5.)

Fourth stage.— Length 1.2 mm., greatest width 0.7 mm. Wing pads of mesothorax extending back over metathorax and first abdominal segment at sides. Prothorax more prominent than in earlier stages. Bases of round-tipped spines several times as long as the spines. A few new spines present on lateral margins of pro- and mesothorax and of abdomen. Color dark brown, except in an irregular band across abdomen just caudad of wing pads and on lateral thirds of prothorax, where it is yellowish. Minute spinules covering entire dorsum, light-colored on the yellowish parts and dark on the brown parts; these spinules present also on bases of round-tipped spines. (Plate LXXIII, 6.)

Fifth stage.— Length 1.6 mm., greatest width 0.96 mm. Wing pads now extending back to fourth abdominal segment at sides, and prothorax still more prominent. A few more spines on tubercles; many of the sharp-pointed spines of the earlier stages now round-tipped; spines present in the earlier stages on lateral margins of segments covered by wing pads have disappeared. Yellowish parts of prothorax increased in size, and distal part of wing pads yellowish, giving the body the appearance of having two light bands across it. Entire dorsal surface covered with minute spinules as in earlier stages. (Plate LXXIII, 7.)

In all stages of the nymphs the larger spines correspond exactly in position and shape with those so excellently described by Morrill (1903) for the oak lace bug, *Corythucha arcuata*. The only distinguishing characters between the nymphs of the two species which the writer has been able to observe are the size and the prevalence of minute awl-shaped spinules on the dorsal surface. Nymphs of *C. bellula* are smaller, and possess more spinules, than those of *C. arcuata*. The larger spines of both species which are mounted on elongate bases seem to have an eversible sac on the tip which gives them a trumpet shape when it is drawn in and a round tip when it is extended.

The natural enemies of these spiny creatures seem to be few. Only the immature stages of several spiders were seen to prey upon them.

The webs of these spiders sometimes cover the infested leaves of a tree and entangle whole colonies of the lace bugs. The adults that survive the winter are comparatively few, so that the first brood of *C. bellula* does little injury.

Cicadellidae (Jassidae)

clitellarius Say, *Thamnotettix*

The adults of *Thamnotettix clitellarius* are of medium size, 5 millimeters long. They are yellow, with black wings which have a prominent yellow spot. A few specimens were found on June 11.

coccinea Först., *Graphocephala*

The adults of *Graphocephala coccinea* are 8 millimeters long, are slender, with a pointed head, and have the wings striped with alternate red and green. They are found on native hawthorns in July and August, but are not common.

curtisii Fb., *Euscelis*

The adults of *Euscelis curtisii* are small, 4 millimeters long, with many narrow yellow and black stripes. Specimens were found on June 23, but were not common.

fitchi VanD., *Idiocerus* (Black apple leaf hopper)

The adult of *Idiocerus fitchi* is 6 millimeters long, is brown or grayish with oblique white marks, and is found on native hawthorns in July and August. The black nymphs were reared on *Crataegus punctata* leaves from June 14 to July 2. The species winters in the egg stage.

lachrymalis Fb., *Idiocerus*

The adults of *Idiocerus lachrymalis* are 8 millimeters long, and are brownish or grayish mottled, with dark venation. They occur on native hawthorns in June and July. They are not common.

lineatus Linn., *Philaenus*

The adults of *Philaenus lineatus* are 6 millimeters long, brownish yellow, stout with a pointed head, and with a small black spot near the apex on the inner margin of the wing. They are found on native hawthorns from July 1 to July 15, but are not common.

mali LeB., *Empoasca* (Apple leaf hopper)

The adults of *Empoasca mali* are $3\frac{1}{2}$ millimeters long, slender, pale green. They are found rarely on Crataegus in late June.

obliqua Say, *Erythroneura*

The adults of *Erythroneura obliqua* are $2\frac{1}{2}$ millimeters long, with the wings striped red and white. They are very abundant on the leaves of native

hawthorns. They hibernate among the fallen leaves under the trees, and hundreds of them were present under *Crataegus punctata* trees in March, 1919. During warm days in winter they hop about over the leaves. Some individuals have pale pink stripes, and others reddish brown. Adults are found feeding on the trees in June and October.

pallidus Fb., *Idiocerus*

A single adult of *Idiocerus pallidus* was taken on June 23, on *Crataegus punctata*. It was 6 millimeters long, and was similar in size and shape to *I. fitchi* but was almost white.

provancheri VanD., *Idiocerus*

The adults of *Idiocerus provancheri* are $5\frac{1}{2}$ millimeters long, and are brown or blackish with an elongate yellow spot on the base of the inner margin of the wing. They are common on the leaves of native hawthorns during June and July. Nymphs in the rearing cages hatched from eggs in *Crataegus punctata* twigs just as the buds were expanding in April. They became adult in three weeks.

querci Fitch, *Empoa*

The small, whitish leaf hoppers known as *Empoa querci* are very abundant on both native and imported hawthorns. The nymphs may be found on the under side of the leaves in late June and July, and again in September. The adults likewise occur on the under side of the foliage in June, August, and late September or early October. They hibernate among the fallen leaves and become active on warm winter days. They are 3 millimeters long, and are pale yellowish white in color.

seminudus Say, *Eutettix*

The adults of *Eutettix seminudus* are $4\frac{1}{2}$ millimeters long, rather stout, and white with a light brown band across the middle of the wings. They are rather common on *Crataegus punctata* and *C. tomentosa* foliage from mid-July to September.

suturalis Fb., *Idiocerus*

The adults of *Idiocerus suturalis* are $5\frac{1}{2}$ millimeters long, and are pallid except for the black inner margin of the wings. They are found on native Crataegus in June and July, but are rare.

vanduzei Gill., *Eupteryx*

The adults of *Eupteryx vanduzei* are $2\frac{1}{2}$ millimeters long, and are slender with a pointed head. The head, the thorax, and the apical part of the wings are brown, and the central part of the body and of the wings is greenish yellow. One nymph was taken on *Crataegus punctata* foliage, and the adult emerged on August 15. The species is rarely found.

vulgaris Fb., *Lamenia*

The adults of *Lamenia vulgaris* are 4 millimeters long, bluish gray, and rather stout. They are abundant on native hawthorns during the last half of June.

Membracidae

crataegi Fitch, *Glossonotus* (Hawthorn tree hopper)

The adults of *Glossonotus crataegi* are fairly common on the branches of native hawthorns during July and early August.

flavicephala Goding, *Ophiderma*

The adults of *Ophiderma flavicephala* are 8 millimeters long, are brown with a yellowish white stripe on each side and across the rear end of the prothorax, and are without a hump. They are rarely found on the branches of *Crataegus punctata* and *C. tomentosa* during June.

taurina Fitch, *Ceresa*

The adults of *Ceresa taurina* are 8 millimeters long, are pale green, and have the prothorax prolonged into a horn on each side of the head. They are found occasionally on the branches of *Crataegus punctata* and *C. neofluvialis* in late July and August. No nymphs were reared to the adult stage on Crataegus, but several nymphs answering the description of this species as given by Hodgkiss (1910) hatched on April 20 and lived through three instars on *Crataegus punctata* foliage.

Aphididae

corrugatans Sir., *Pemphigus* (Woolly thorn aphis)

A few colonies of the flocculent greenish aphids of the species *Pemphigus corrugatans* were found in early June on *Crataegus punctata*. They live on the under side of the leaves and curl the leaf margins downward.

crataegi Monell, *Macrosiphum*

The apterous females of *Macrosiphum crataegi* may be found from late May until October on the native hawthorns at Ithaca, and during July and August the species may become so abundant as to seriously injure the

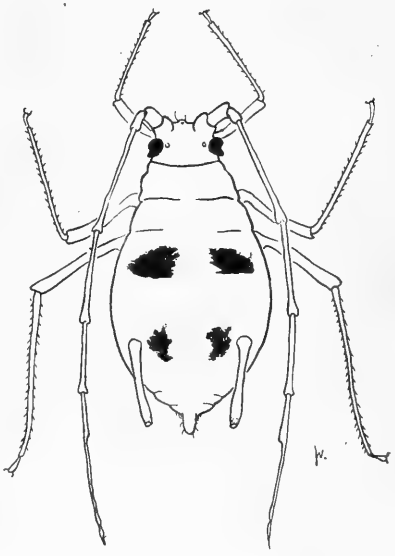


FIG. 108. MACROSIPHUM GRATAECI

trees. During the summer of 1919 the writer saw a small *Crataegus pruinosa* tree killed and a very large *C. punctata* tree almost entirely defoliated due to the sucking of sap by myriads of these aphids. They are rather large, yellowish green aphids, with long cornicles, and their most easily recognizable character is the presence of four dark green spots arranged in a rectangle on the dorsal side of the abdomen (fig. 108). The entire life history is passed on Crataegus trees. The black winter eggs are placed on the twigs and the smaller branches. They begin to hatch in May, after the leaves are well opened. The young aphids move to the lower surface of the leaves, and their feeding, as the colony increases, causes the leaves to curl downward.

In late June an alate brood appears and migrates to near-by branches or trees to start new colonies. It is after this brood appears that the species becomes so injurious.

crataegifoliae Fitch, *Aphis*

In early May, 1918, the *Crataegus coccinea* trees at Ithaca began to show the terminal rosettes of curled leaves caused by *Aphis crataegifoliae*. The rosettes turned red, and the aphids within them also were red. The infested branches remained deformed and somewhat stunted throughout the season, although the aphids departed from the trees about May 20 to seek leguminous hosts. No aphids of this species were observed the next year.

FIG. 109. ERIOSOMA LANIGERA ON HAWTHORN

lanigera Hausm., *Eriosoma* (Woolly aphis)

The woolly aphids first become noticeable in early June as small white spots on the tender twigs of Crataegus. In a favorable season such as the summer of 1918, they become very conspicuous and cover entire branches by late summer (fig. 109). The writer has not found the roots of Crataegus infested.

pomi De Geer, *Aphis* (Green apple aphis)

During June and July the succulent sprouts of European and native hawthorns are badly infested by green apple aphids. Whenever the weather becomes unfavorable for their enemies they increase rapidly and infest entire trees or hedges, but fair weather checks them again.

prunifoliae Fitch, *Rhopalosiphum* (Apple bud aphis)

The dark green stem mothers of the species *Rhopalosiphum prunifoliae* begin to appear on the buds of native hawthorns as soon as the bud scales have separated enough to show the green leaves within. The colonies increase during April and early May, doing some damage to the young leaves and buds, but before June they migrate from the trees to grasses and are not often found on the trees between early June and late autumn. The winter eggs are laid on hawthorn twigs and buds.

Coccidae

corni Bouché, *Lecanium* (European fruit lecanium)

The species *Lecanium corni* is often very abundant on the lower side of branches of native hawthorns, and occasionally a branch is found to be almost entirely covered with these scales. Lower or inner branches that receive a scanty supply of light appear to be killed by them. The young, flat scales are sometimes very plentiful on the leaves in late summer.

furfura Fitch, *Chionaspis* (Scurfy scale)

The flat, whitish scale known as *Chionaspis furfura* is very common and noticeable on the bark of all Crataegus species which the writer has observed. The small, elongate, white, male scales are often very abundant on the leaves and bark of *Crataegus punctata.* The injury caused by these scales is not noticeable.

perniciosus Comst., *Aspidiotus* (San José scale)

Although the San José scale is fairly common on all species at Ithaca, it does not seem to increase rapidly enough to become injurious. It is more commonly found on the smooth bark of young trees than on old, rough-barked trees.

ulmi Linn., *Lepidosaphes* (Oyster-shell scale)

The oyster-shell scale is common on the bark of native and European hawthorns, and a few badly infested branches have been found. Generally, however, this species seems to be unimportant as a pest of Crataegus.

vitis Linn., *Pulvinaria* (Cottony scale)

The species *Pulvinaria vitis* is occasionally found on the twigs and branches of native hawthorns, but is not very abundant.

THYSANOPTERA

Thrypidae

tritici Fitch, *Euthrips*

Nymphs and adults of *Euthrips tritici* are very common in flowers and flower buds of native hawthorns in April and May. Many flower buds fail to open, and inside of them are found from one to a dozen or more of these thrips. They were exceedingly abundant in the Cornell University arboretum in 1918, and very few hawthorns there bore fruit that year.

COLEOPTERA

Elateridae

dubitans Lec., *Limonius*

The beetles of the species *Limonius dubitans* occasionally are found eating leaves of native hawthorns in late May and early June. On May 31, 1919, one of these click beetles was found on a *Crataegus pruinosa* leaf where it had been feeding, and was attacked by an adult pentatomid, *Apeteticus modestus* Dallas. The latter had its beak inserted into the beetle, which died while being carried to the laboratory.

pubescens Melsh., *Agriotes*

The beetles of *Agriotes pubescens* were eating the leaves of *Crataegus punctata* on May 23. The species is not common.

Melanotus sp.

The beetles of *Melanotus* sp. were eating the leaves of *Crataegus punctata* on June 6 and June 8. The species is not common.

Buprestidae

aerosus Melsh., *Brachys*

The beetles of *Brachys aerosus* were found feeding on *Crataegus punctata* leaves in warm sunlight from May 30 to June 20. There were commonly two or three to a leaf, feeding on the upper surface and cutting small holes through the leaf. As many as fifty of the beetles were found on one tree, while neighboring trees had none. They are from 4 to 5 millimeters long, and are brown and gold in color.

Scarabaeidae

elongata Fabr., *Dichelonycha*

The beetles of *Dichelonycha elongata* were found feeding on *Crataegus punctata* foliage, six being seen on one tree on May 31. A seventh beetle was killed by three adult pentatomids of the species *Apeteticus modestus*, which were feeding on its body.

testacea Kirby, *Dichelonycha*

The beetles of *Dichelonycha testacea* were found on *Crataegus tomentosa* foliage on May 29 and July 1. They cut irregular patches from the edge of the leaf. The species is not common.

Chrysomelidae

borealis Shev., *Dibolia*

The green flea beetles of the species *Dibolia borealis* are $2\frac{1}{2}$ millimeters long. They feed on native hawthorn foliage in May, as soon as it is expanded. They hibernate beneath bark scales on the trunk and the branches, and when warmed in the hand in February they very soon become active.

carinata Germ., *Haltica*

The metallic violet or green flea beetles of the species *Haltica carinata* are 4 millimeters long. They feed on foliage of native hawthorns in June. They are not common.

cucumeris Harris, *Epitrix*

Tiny shining bluish beetles less than 2 millimeters long, of the species *Epitrix cucumeris*, were found feeding on *Crataegus punctata* foliage in June. The species is not common.

helxines Linn., *Crepidodera*

The shining greenish flea beetles of the species *Crepidodera helxines* are 3 millimeters long. They feed on the foliage of native hawthorns and are frequently so numerous as to cause considerable injury. They are found feeding in May, June, July, and August, but are most abundant in late May and in June. The beetles hibernate under bark scales on the trunk and the larger branches, where many of them die from the attack of a white fungous growth before spring.

marginalis Ill., *Systena*

Yellowish brown, slender flea beetles 4 millimeters long, of the species *Systena marginalis*, were found in August and early September eating holes in leaves of native hawthorns. The species is fairly common.

villosula Melsh., *Xanthonia*

The stout brownish or black beetles of the species *Xanthonia villosula* are 4 millimeters long. They were found feeding on the leaves of *Crataegus punctata* from late June to early August. Occasionally they are so abundant as to completely riddle the foliage of a tree with the holes they cut in feeding (Wellhouse, 1919). Feeding punctures are shown in figure 110, on the following page.

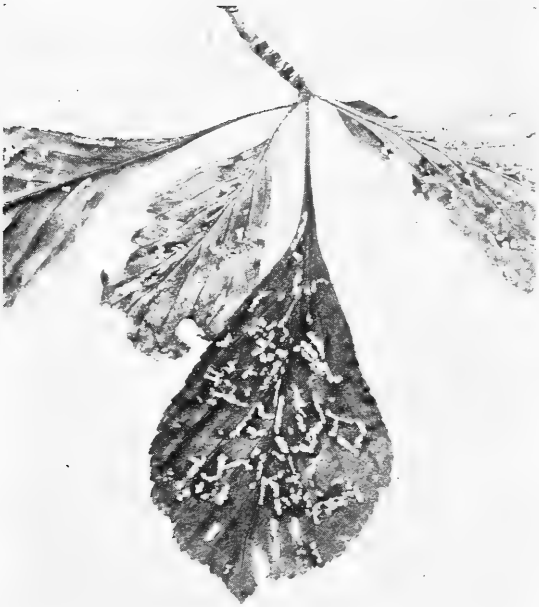


FIG. 110. FEEDING PUNCTURES OF XANTHONIA VILLOSULA IN LEAVES OF CRATAEGUS PUNCTATA

Curculionidae

crataegi Walsh, *Conotrachelus* (Quince curculio)

The square-shouldered brown beetles of *Conotrachelus crataegi* were found puncturing the fruit of Crataegus for feeding and oviposition in July and August, 1918, and in late May and June, 1919. The early months of 1919 were much warmer than those of 1918 at Ithaca, and this probably is the cause of the great variation in the time of their appearance. The larvae develop within the haws, feeding on the pulp surrounding the large, stony seeds. A larva commonly eats about one-half of the entire pulp of the fruit before emerging in the autumn, when it leaves the fruit by a large, round, exit hole. It then burrows down two or three inches in the soil and spends the winter as a larva curled in a smooth-walled earthen cell. In June, 1918, the writer found ninety-six larvae in the soil beneath one *Crataegus punctata* tree. Some of them pupated in June and others in July. They are very common on all the native hawthorns.

nebulosus Lec., *Anthonomus* (Hawthorn blossom weevil)

One of the most interesting and injurious of the insects found on the hawthorns is *Anthonomus nebulosus*, a member of a very destructive genus of blossom weevils. Its mode of life resembles in a general way that of the Mexican cotton boll weevil, *A. grandis*, and is almost identical with that of the European apple-blossom weevil, *A. pomorum* (Theobald, 1909: 104–110).

The original description of *A. nebulosus* is to be found in the Proceedings of the American Philosophical Society (Leconte, 1876), and a more complete description is given by Dietz (1891). In the present account it is

sufficient to say that *A. nebulosus* is a brown or grayish oval beetle, from 3.75 to 4.25 millimeters long, generally with a whitish, V-shaped mark on the fore part of the elytra, with a long, slender, curved beak, and the front femur having two teeth on its apical part, one large and the other small (Plate LXXIV, page 1070).

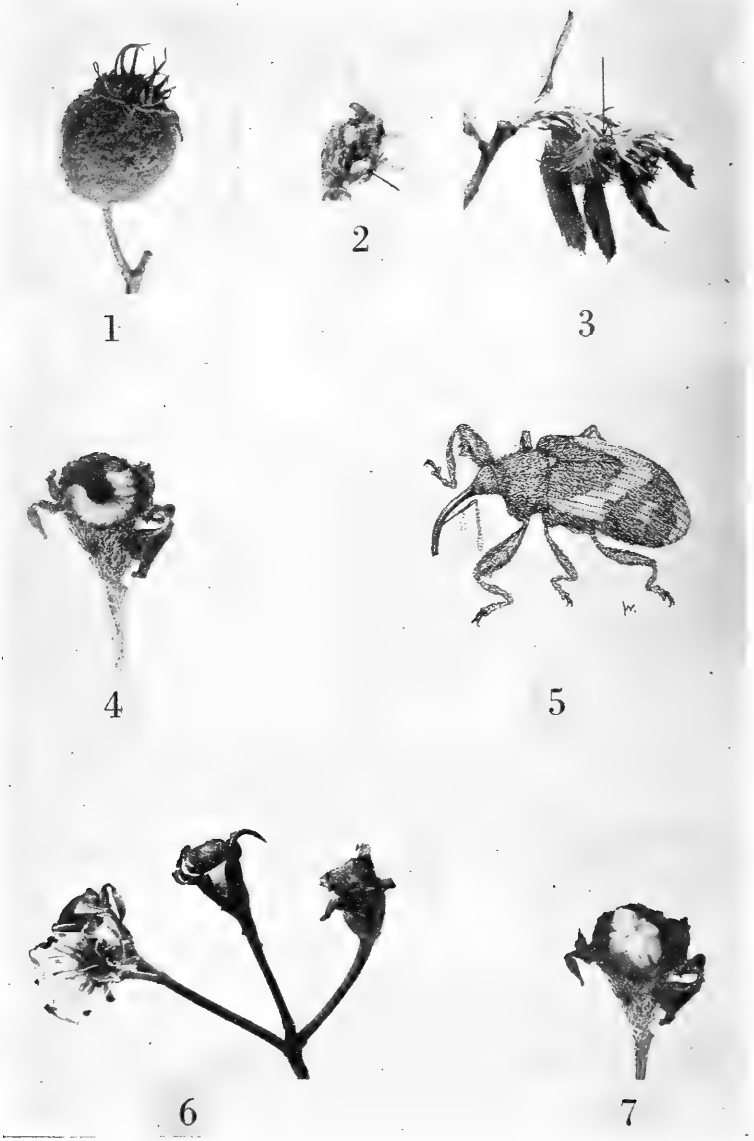
The species has been found in New York, New Jersey, Michigan, Indiana, Missouri, Arkansas, and Louisiana, and therefore it seems probable that it is present wherever its hosts are found east of the Rocky Mountains. Although Dietz considers this species to be more characteristic of the European fauna than of our own, no record can be found of its occurrence in Europe or elsewhere outside of this country.

Its hosts include a number of the larger-flowered species of hawthorns, such as *Crataegus punctata*, *C. brainerdi*, *C. pruinosa*, and *C. mollis*. The smaller-flowered species, such as *C. oxyacantha*, are not selected by the beetles for oviposition, probably because there is not space enough for the full development of the larva within the bud.

The injury caused by the hawthorn blossom weevil is most apparent while the trees are in full bloom. At that time the infested blossoms are brown and remain closed. On badly infested trees fully fifty per cent of the blossoms may be in this condition and the trees present a scorched appearance. As the young fruit begins to set, the infested blossoms commonly fall to the ground, but they may sometimes be seen on the trees even after the beetles have emerged in June.

The beetles come out of hibernation and appear on the branches of the hosts about mid-April, feeding ravenously on the buds, which are showing green. It is not uncommon to see a beetle with feet braced and beak inserted up to the eyes in a bud while it hurriedly eats the tender leaves within. As soon as all the food within reach of the entrance hole is eaten, the beetle seeks another bud on the twig and repeats the process. The puncture in the bud is round, is 0.3 millimeter in diameter, and turns dark as soon as the beak is withdrawn. The presence of the beetles may be detected by these dark round holes in the buds before the egg-laying period arrives. The beetles continue to feed on the buds during suitable weather until the clusters have separated enough for oviposition in the blossoms.

During cool weather the beetles remain inactive, generally in the axils of the twigs with their heads down. A few observations on the relation of temperature to their activities were made, and these indicate that the beetles remain inactive while the temperature is below 50° F. The optimum temperature is from 60° to 70°, and when it is raised to 78° the beetles rush about like mad, attempting to oviposit in every bud. Under most conditions they seem reluctant to fly, but when placed on distasteful food they fly away. They continue their activities on cloudy or rainy days and at night if the temperature is sufficiently high.



ANTHONOMUS NEBULOSUS

1, Feeding punctures of beetles in hawthorn fruit. 2, Egg in blossom bud. 3, Female ovipositing in blossom bud. 4, Flower with petals removed to show full-grown larva in its natural position. 5, Adult beetle. 6, Three flower buds containing larvae, and one normal blossom. 7, Flower with petals removed to show pupa in its natural position

The period between the opening of the blossom clusters and the opening of the blossoms themselves is the time of oviposition, and the length of this period probably influences the amount of injury to a considerable extent. If it is prolonged by cool, cloudy weather, then eggs may be placed in more of the blossoms before they open. In central New York the oviposition period is about May 15.

After selecting a suitable blossom bud, the female makes a hole in the side of the calyx with her beak. Then, turning around, she thrusts the egg into the hole with her ovipositor, and moves to another bud to repeat the process. A clear liquid fills the hole where the egg is thrust in, which soon hardens and seals the opening completely. The act of oviposition requires about ten minutes when the temperature is 68° or 70°, but it requires an hour at 54°.

The egg is pearly white, 0.6 millimeter long, 0.36 millimeter wide, elliptical, generally the same size at both ends but when tucked in tightly between the anthers it may be narrower at one end to conform to the space it fills. It is of almost the same size and color as the anthers and is difficult to distinguish from them. The corium is smooth, unsculptured, and delicate, drying and collapsing when exposed to the air for one hour.

After about a week the young, white, curved, legless larva is found within the bud. It feeds on the anthers, and, as it grows, consumes all the internal parts of the flower but leaves intact the wall of the receptacle and the closed petals which form the roof of its house. The petals become stiff as if they were starched, and do not shrink away as they turn brown. After feeding for a couple of weeks the larva is dirty white, is from 6 to 8 millimeters long, is still legless, has a small brown head, and lies in a curved position. At about this time it molts and changes to a white, free pupa 6 millimeters long, with a dark caudal spine, two dark prominent spines on the apex of the head, and several smaller spines farther back on the head. After pupating during a week or a little longer, the beetle makes a hole in the top or the side of its house with its beak, and emerges.

It begins to feed a few minutes after emergence, choosing for its food the first young thorn or fruit in its pathway as it wanders along the branch. The thorns of the current season's growth seem to be a very attractive food. A hole is drilled near the base of the thorn, and the beetle spends hours with its beak inserted in the hole completely up to its eyes, prying and straining to enlarge the cavity within the thorn. The round hole at the base of a thorn does not heal during the season's growth, and the presence of such holes will indicate at any time of the year the presence of the blossom weevils. The beetles attack the fruit also and make several round holes in a single fruit before seeking another. The holes become brown almost immediately. The writer has never found

the beetles eating leaves or tender twigs, but they sometimes feed on the succulent globular leaf galls of cecidomyiid larvae. They will puncture and feed on young apples in the cages when fresh haws are not to be had, but the writer has found none feeding on apples in the field.

After feeding for a week or ten days the beetles may be found in copulation on the branches, and a week or so later, as warm July weather comes, they disappear from the trees. Those kept in breeding cages remained hidden in fallen curled leaves and hollow twigs on the ground all summer and winter without feeding until the next spring. A search for their hiding places in the field revealed a score of the beetles inclosed in curled, dried leaves on the ground beneath their host trees.

The life cycle may be summarized as follows: The immature stages (egg, larva, and pupa) are completed within the closed blossom in from twenty-seven to thirty-five days, and the remainder of the year is passed in the adult stage. The adults feed on thorns and fruit for two or three weeks after emerging from the blossoms, and then remain quiescent among fallen leaves on the ground until the next spring, when they feed for about a month on the buds before ovipositing. Soon after oviposition the beetles die. In New York the eggs are laid about mid-May and the beetles emerge from the blossoms in June. W. D. Pierce, in a letter to the writer, says the beetles emerge in late March and early April in Louisiana. The time of their development in different latitudes is dependent on the opening of the hawthorn blossoms in those latitudes.

A number of natural enemies of the blossom weevil have been observed. Various birds, especially sparrows, pick open the brown blossoms to eat the larvae and the pupae. Pierce (1912:77) found the weevils to be parasitized by *Catolaccus hunteri* and *Sigalphus* sp. The writer has bred another chalcid, *Habrocytus piercei* Cwfd., from the larva of the weevil, the adult parasites emerging on June 16 and 17.

quadrigibbus Say, *Tachypterus* (Apple curculio)

The four-humped brownish beetles of the species *Tachypterus quadrigibbus* were found occasionally feeding on the fruit of native hawthorns in June. Fruits of *Crataegus punctata* were put into rearing cages on June 25, and from these fruits five adults of this species emerged on July 15 and July 18.

LEPIDOPTERA

Papilionidae

turnus Linn., *Papilio* (Tiger swallowtail)

The green larvae of *Papilio turnus*, with their peculiar eye spots, were found feeding on the foliage of native hawthorns from June 20 to August 2. The species is not very common.

Saturniidae

io Fabr., *Automeris*

The eggs of *Automeris io* are not uncommon on the under side of hawthorn leaves in late June and in July. They are very characteristic and conspicuous. A cluster of eggs may consist of a dozen or more, each large and creamy white with a dark blue dot on the distal end. The larvae feed in colonies on the foliage during July, August, and September. They are at first dark, then green, and are always covered with a mass of dark, stinging spines.

Arctiidae

caryae Harris, *Halisidota* (Hickory tussock moth)

The black-and-white-tufted caterpillars of the species *Halisidota caryae* are fairly common on native hawthorns during August.

tesselaris A. and S., *Halisidota*

The caterpillars of *Halisidota tesselaris* are similar to those of *H. caryae* and are found occasionally on the foliage with them, but are not so common.

textor Harris, *Hyphantria* (Fall webworm)

A single colony of larvae of *Hyphantria textor* was feeding on *Crataegus pruinosa* on July 31, 1918. An egg cluster which was probably of this species hatched on June 19, and the young larvae fed on *C. punctata* leaves for a few days and then died.

Noctuidae

americana Harris, *Acronycta*

The larvae of *Acronycta americana* are green, with an abundant covering of yellowish white hairs and a few long pencils of black hairs. They were found feeding on the leaves of native hawthorns in late June and July. The species is not common.

dactylina Grote, *Acronycta*

The larvae of *Acronycta dactylina* are entirely covered with yellowish white hairs and have three long pencils of black hairs. They were feeding on the foliage of *Crataegus punctata* from August 15 to September. The species is not common.

luteicoma G. and R., *Acronycta*

The larvae of *Acronycta luteicoma* are black, with tufts of white hairs on segments 3 to 6 and tufts of black hairs on the other segments. They were found feeding on *Crataegus punctata* leaves from June 23 to July 22. The species is not common.

occidentalis G. and R., *Acronycta*

The larva of *Acronycta occidentalis* is hairy, with a dark head and dorsal stripes. The remainder of the body is at first whitish but in later stages is reddish. Larvae of this species were feeding on *Crataegus punctata* foliage from August 13 to September. The species is not common.

pyramidoides Guen., *Amphipyra*

The larva of *Amphipyra pyramidoides* is green, with a white dorsal and two yellow lateral stripes, and is found feeding on native hawthorn leaves in May. One larva constructed a silken cocoon among dead leaves on the ground on June 2 and the moth emerged on July 18. The species is not common.

radcliffei Harv., *Acronycta*

The larva of *Acronycta radcliffei* is greenish or black, has a dorsal line of green or brown with faint yellow and red lines, has a hump on segment 12, and is sparsely hairy. It feeds on the leaves of *Crataegus punctata* from June 29 to July 22. The species is not common.

superans Guen., *Acronycta*

The larva of *Acronycta superans* is green, with a black dorsal line widened into a spot on several abdominal segments and with the last segment angularly elevated. There are few hairs on the body. It was feeding on *Crataegus punctata* leaves from June 9 to July 1, and pupated in a silken cocoon among leaves and decayed wood on the ground. The moth emerged on July 23. Only one larva was found.

Notodontidae

concinna A. and S., *Schizura* (Red-humped apple caterpillar)

The brownish, red-humped larvae of *Schizura concinna* feed on leaves of native hawthorns during July, August, and early September. Occasionally they defoliate several branches of a tree, but they are not generally injurious as is *Datana ministra*. They seem to prefer apple to hawthorn. On July 27, 1918, a count was made of the infested trees in several thickets where seedling apples and hawthorns were growing together. Although the hawthorns were much more numerous than the apples, the latter had forty-six infested trees while the former had only three.

manteo Doub., *Heterocampa*

The larva of *Heterocampa manteo* is bright green marked with red. It was found feeding on the foliage of native hawthorns in late June and in July. The species is not very common. One larva taken from a *Crataegus punctata* tree on August 15 continued to feed in the cage until September 2, when it wandered away to find a suitable place for spinning its cocoon.

ministra Dru., *Datana* (Yellow-necked apple caterpillar)

One of the most destructive species to both native and European hawthorns during the past few years has been *Datana ministra*. Very few trees have escaped without at least one colony of these yellow-necked, black-bodied, gray-haired caterpillars feeding on a branch in July and August. Many trees have had an entire branch stripped bare of leaves, and occasionally a whole tree has been defoliated.

The light brown moths appeared and were found ovipositing during June and July. The clusters of white eggs, each cluster containing from 25 to 100, were deposited on the lower side of the leaves and were a common sight in July. The larvae of a colony begin to feed at the tip of a branch and migrate toward its base as they grow, leaving the bare branch behind them. As they become larger they scatter to adjacent branches and feed singly or by twos and threes. They become full-grown and enter the soil in September.

Several observations were made to determine whether the larvae prefer hawthorn to apple. When confined in cages they eat one as readily as the other. In the natural uncultivated areas where hawthorn, apple, and pear grow wild, however, it was noticed that the colonies of larvae were commoner on hawthorn than on the other trees. In one field containing 50 hawthorn, 39 apple, and 17 pear trees, 79 colonies of larvae were counted. Of these colonies 56 were on hawthorn, 15 on apple, and 8 on pear.

Lymantriidae

leucostigma A. and S., *Hemerocampa* (White-marked tussock caterpillar)

The larva of *Hemerocampa leucostigma*, with its bright red head, its red tubercles on segments 6 and 7 of the abdomen, its four white tussocks, and its three long, black pencils of hairs, is a common sight on both native and European hawthorns. It feeds on the foliage during June and July, and the hairy cocoons are common on the branches in winter.

Lasiocampidae

americana Harris, *Epicnaptera*

The large larva of *Epicnaptera americana* is gray with white spots and two red bands above, and orange with a row of lateral diamond-shaped black spots below. It feeds at night on *Crataegus punctata* foliage in July and August. The species is not common.

americana Fabr., *Malacosoma* (Apple tent caterpillar)

During the years 1917 to 1920, only the old egg masses of *Malacosoma americana* were found on the twigs of hawthorns about Ithaca. Only two colonies of larvae were seen on the favorite host, wild cherry, and only one colony on apple.

Geometridae

cognataria Guen., *Lycia*

The larva of *Lycia cognataria* is green and is 4½ centimeters long. It has two pairs of prolegs. On its head are blunt horns, and it bears a prominent red tubercle on the next to the last segment. It feeds on *Crataegus punctata* and *C. pruinosa* foliage in July. It is not a common species.

magnarius Guen., *Ennomos*

A moth of *Ennomos magnarius* emerged from a brown silken cocoon on a twig of *Crataegus pruinosa* on September 30. Eggs were found on a *C. punctata* twig on November 12. The brownish larvae, 5 centimeters long, were found occasionally in May and June.

pometeria Peck, *Alsophila* (Fall cankerworm)

The small greenish or brownish larvae of *Alsophila pometeria* are fairly common on native hawthorns in May.

subsignarius Hüb., *Ennomos*

The white moths of *Ennomos subsignarius* emerged on July 6 and July 18 from pale yellowish pupae which were found tied with silk between the leaves of *Crataegus punctata*. A few of the brown and red larvae were found feeding on the foliage of native hawthorns in May.

tiliaria Harris, *Erranis* (Lime-tree spanworm)

The yellow-and-black-striped larvae of *Erranis tiliaria* are common on native hawthorn foliage in May and June.

titea Cram., *Phigalia*

Two larvae of *Phigalia titea* were found feeding on *Crataegus punctata* leaves on June 2 and June 5.

vernata Peck, *Paleacrita* (Spring cankerworm)

The larvae of *Paleacrita vernata* are common on foliage of native and European hawthorns in May and early June.

Sesiidae (Aegeriidae)

scitula Harris, *Sesia*

A single *Crataegus punctata* tree about eight years old and 5 feet high was killed by the larvae of *Sesia scitula*. The trunk was entirely girdled by four larvae which tunneled beneath the bark two inches above the soil. The sapwood was only slightly indented by their burrows around it. They pupated during June in silken cocoons covered with frass within the burrows, and the moths emerged from July 18 to July 24. In emerg-

ing, the moth pushes through one end of the cocoon, and then sheds the pupal skin while protruding about two-thirds of its length beyond the cocoon. The black, clear-winged moth has a broad and a narrow band of yellow across the abdomen.

Pyralidae

indigenella Zell., *Mineola* (Leaf crumpler)

The cornucopia-like winter cases of *Mineola indigenella*, a leaf crumpler, are easily seen on almost any hawthorn tree during the winter, attached firmly to the twigs and the branches and often with partly eaten leaves attached. The larvae carry the cases with them and feed on the leaves in April and May. They pupate within the same cases attached to twigs in June, and at Ithaca the moths emerge in late June.

Tortricidae

argyrospila Walk., *Archips* (Fruit-tree leaf roller)

The greenish larvae of *Archips argyrospila*, with their black heads and shields, are fairly abundant on the foliage of native hawthorns during May and are found occasionally in June. They tie together a cluster of leaves and feed on a leaf within the cluster. Moths emerged from the larval nests in late June and early July.

chionosema Zell., *Olethreutes*

The pale green larvae of *Olethreutes chionosema* fold the leaves of native hawthorns and feed on the upper surface of the leaves within the fold. Each larva folds a single leaf at a time. They are fairly common on the hawthorns and apple trees about Ithaca during May. The moths fly during June after pupating within the folded leaf. A few moths taken on August 14 and 15 seem to indicate a second brood. The moth (fig. 111) is brownish, with a large white spot on the costal edge of the fore wing, and has a wing expanse of from 15 to 16 millimeters.

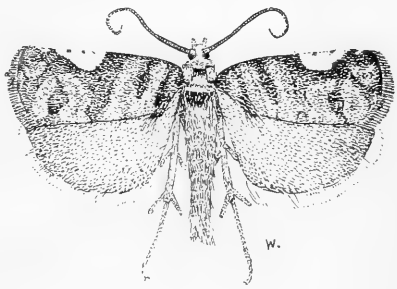


FIG. 111. OLETHREUTES CHIONOSEMA

nubeculana Clem., *Ancylis*

The greenish larvae of *Ancylis nubeculana* were found in late summer in rolled leaves of *Crataegus punctata*. They pupated in May and the moths emerged from June 8 to June 18. The species is not very common.

ocellana Fabr., *Tmetocera* (Bud moth)

The brownish larvae of *Tmetocera ocellana* are commonly found in the partly opened leaf buds in April and May, on both native and European hawthorns. The moths emerge from the larval nests in June and early July.

prunivora Walsh, *Laspeyresia* (Lesser apple worm)

The small white caterpillars of *Laspeyresia prunivora* are very common in the fruit of many native hawthorns in late summer. They eat most of the pulp from one side of the fruit, causing the skin to sink in there. The larvae of the second generation sometimes remain in the fruit all winter, living within a mixture of silk and pellets of frass. Others spin silken hibernacula under the bark of the trunk very similar to those of the codling-moth larvae but smaller. They pupate within the hibernacula in the spring and the moths emerge in May and June. In the laboratory they emerged in March. Moths of the first generation were taken in the field from August 15 to August 30.

quadrifasciana Fern , *Eulia*

The yellowish larvae of *Eulia quadrifasciana* tie together with silk the leaves of terminal clusters on *Crataegus punctata* in May. They pupate within the larval nests and the moths emerge in early June. The moth is yellow and orange, with darker oblique bands on the fore wings. The species is not very common.

rosaceana Harris, *Cacoecia* (Oblique-banded leaf roller)

Clusters of leaves tied together by the larvae of *Cacoecia rosaceana* are fairly common on all native hawthorns in May and July. The green-striped larva, with its brown head and shield, is generally found on a single leaf under a slight web, feeding on one side of the leaf only. When full-grown the larva ties a cluster of leaves together to pupate within. Moths emerged from these nests from May 26 to June 30, and a second brood emerged from August 1 to August 15.

Yponomeutidae

oreasella Clem., *Argyresthia*

The small, green, black-headed larva of *Argyresthia oreasella* bores through a terminal leaf bud down into the twig and makes a hole in the side of the twig about $\frac{1}{2}$ inch from the tip, through which the frass is cast out of the burrow. When disturbed the larva runs quickly out of either the hole in the twig or the hole in the bud, to escape. Infested twigs wilt soon after the larva has left the burrow, and then become brown and dry, giving the tree a fire-blighted appearance (fig. 112). Larvae of this species were found in many native hawthorn twigs in May. They leave the

twigs when full-grown, and spin a parchment-like white cocoon surrounded by an open layer of lacework attached to the surface of a leaf. The moths emerged from June 15 to June 30. A few moths taken in the field on August 16 seem to indicate a second brood. The moth is slender, and is white with oblique gold bands on the fore wings while the hind wings are dark gray. Its wing expanse is about 13 millimeters. It has a peculiar habit of standing on its head when at rest on the leaves or the bark.

FIG. 112. TERMINAL OF HAWTHORN TWIG DESTROYED BY LARVA OF ARGYRESTHIA OREASELLA

Elachistidae

fletcherella Fern., *Coleophora* (Cigar case-bearer)

The brown, cigar-shaped cases of the larvae of *Coleophora fletcherella* are common on all the hawthorns throughout the growing season. They have been specially abundant and injurious on trees and hedges of *Crataegus oxyacantha*, the European hawthorn, during the years 1918 and 1919. The moths emerged from the cases in late June and July.

malivorella Riley, *Coleophora* (Pistol case-bearer)

The curved cases of the larvae of *Coleophora malivorella* are fairly common on hawthorns but not so abundant as those of *C. fletcherella.*

splendoriferella Clem., *Coptodisca* (Resplendent shield-bearer)

The small, yellowish brown, winter shields of *Coptodisca splendoriferella* are rather commonly found attached to the bark and swinging in the wind on the branches of native hawthorns, and their blotch mines in the leaves are not uncommon.

Lyonetiidae

pomifoliella Clem., *Bucculatrix* (Ribbed-cocoon-maker of apple)

The elongate, white, ribbed cocoons of *Bucculatrix pomifoliella* are common on native hawthorns and are rather noticeable in winter, when the trees are leafless. The moths emerge in late May.

Cosmopterygidae

curvilineella Chamb., *Blastodacna* (Hawthorn fruit miner)

The larvae of *Blastodacna curvilineella* are very commonly found tunneling in the fruit of native hawthorns in late summer. They become full-grown in September and October, when they leave the fruit and burrow into the ends of dead twigs or other decaying wood to hibernate. The hibernation cavity is lined with silk, and in the early spring pupation takes place there. The moths emerge in May and June. They are gray, with two or three indistinct dusky longitudinal short streaks on the wings, and have a wing expanse of 1 centimeter.

The larva is from 9 to 10 millimeters long. In color it is yellowish white, with a brown head and thoracic legs, red spots near the spiracles, more or less blackish among the setae on the dorsum of each segment but especially noticeable on the prothorax and the anal segment, and many patches of black setae arranged as shown in figure 113. It feeds on the pulp of the fruit and leaves many brown pellets of excrement in the burrow behind it. Often one whole side of a fruit is mined out, leaving only the skin to cover it.

FIG. 113. LARVA OF BLASTODACNA CURVILINEELLA

The moths have been bred from larvae in *Crataegus pruinosa*, *C. neofluvialis*, and *C. macracantha*, and the larvae have been found in a number of other native hawthorns. The moth has been reported by Chambers from Kentucky (1872) and from Canada (1875), and therefore it probably occurs throughout the Eastern States.

A closely related European species, *B. hellerella* Dup., feeds in the fruit of hawthorns and also bores into young apple shoots (page 1116).

DIPTERA

Cecidomyiidae (Itonididae)

absobrina Felt, *Rhizomyia*

crataegifolia Felt, *Lestodiplosis* (Hawthorn fringed-cup gall)

Adults of both *Rhizomyia absobrina* and *Lestodiplosis crataegifolia* have been reared by Dr. Felt from larvae in the galls. The galls are green and cup-shaped, and are covered externally with round-tipped spines 4 or 5 millimeters in diameter and about the same in height (figs. 114 and 115). They occur on the larger veins and petioles of leaves and on the ends of young twigs of *Crataegus pruinosa* and *C. macracantha*. Several galls are commonly found in a group on the same or adjoining leaves. Those on the leaves are on the upper side, but extend through the leaves to form a smooth, semi-globular swelling on the lower side.

FIG. 114. HAWTHORN FRINGED-CUP GALLS

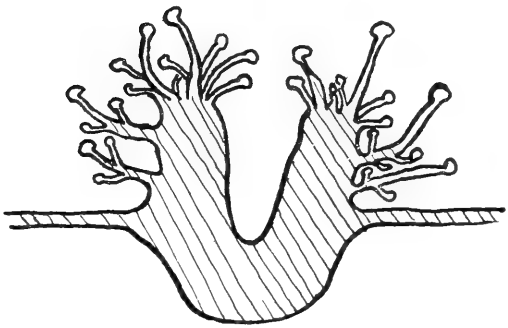


FIG. 115. CROSS SECTION THROUGH A HAWTHORN FRINGED-CUP GALL

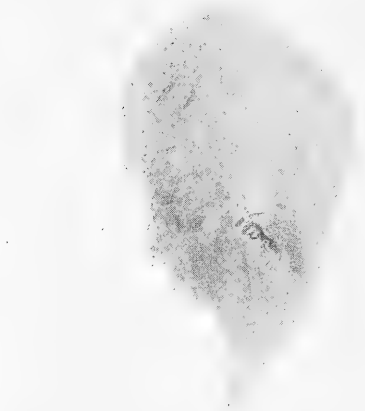


FIG. 116. THORN COCKSCOMB GALL

White larvae, 3.5 millimeters long and with a distinct brown breast-bone, were found, one in each gall, in June.

crataegifolia Felt, *Hormomyia* (Thorn cockscomb gall)

Green or red cockscomb-like galls (figs. 116 and 117) produced by *Hormomyia crataegifolia* are found on the upper or the lower side of leaves of *Crataegus pruinosa*, *C. macrosperma*, and *C. coccinea*. They are often in groups on a leaf or a cluster of leaves, and each gall includes a vein. The gall is from 8 to 12 millimeters long and 5 millimeters high, and is open to the outside by a long, narrow slit on the opposite side of the leaf. These galls are found in August.

venae Felt, *Lobopteromyia* (Thorn vein gall)

Round or oval, thick-walled, green galls (figs. 118 and 119) from 5 to 8 millimeters long, produced by *Lobopteromyia venae*, are found on either the upper or the lower surface of leaves of *Crataegus punctata*. The gall opens on the opposite side of the leaf by a narrow slit which extends the entire length of the gall in the direction of the vein. It always includes one of the larger veins. The galls are fairly abundant in June, when several may be found on one leaf and all the leaves in a cluster are deformed.

Cecidomyia sp. (a. 1840 Felt) (Thorn spindle gall)

Red or green, elongate spindle-shaped galls (figs. 120 and 121) 2 millimeters wide and from 5 to 10 millimeters long, produced by *Cecidomyia* sp., are found on either side of the leaves of *Crataegus punctata*. The gall opens by

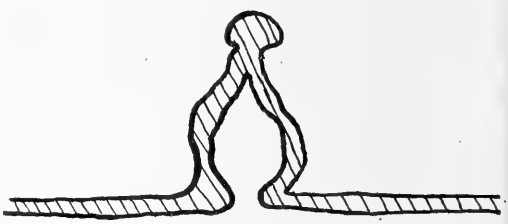


FIG. 117. CROSS SECTION THROUGH A THORN COCKSCOMB GALL

FIG. 118. THORN VEIN GALLS

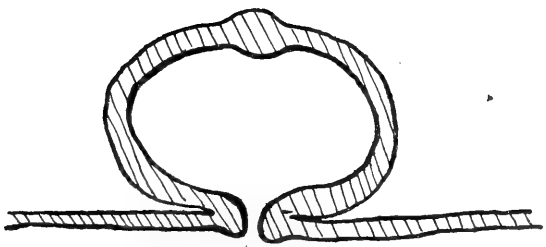


FIG. 119. CROSS SECTION THROUGH A THORN VEIN GALL

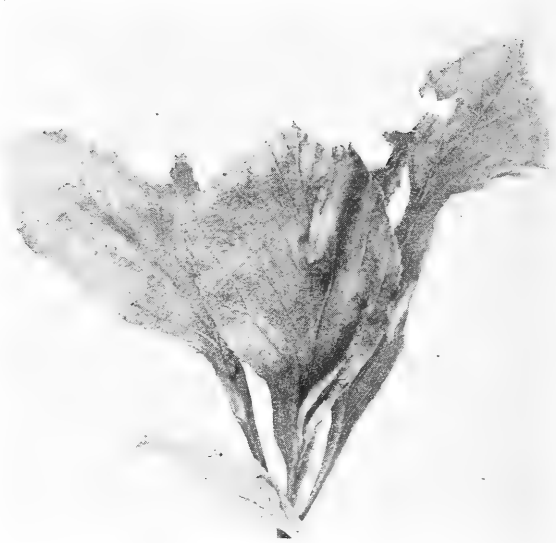


FIG. 120. THORN SPINDLE GALLS

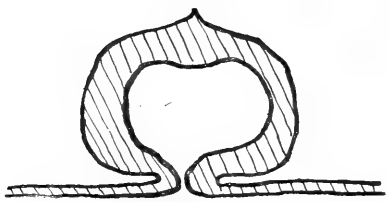


FIG. 121. CROSS SECTION THROUGH A THORN SPINDLE GALL

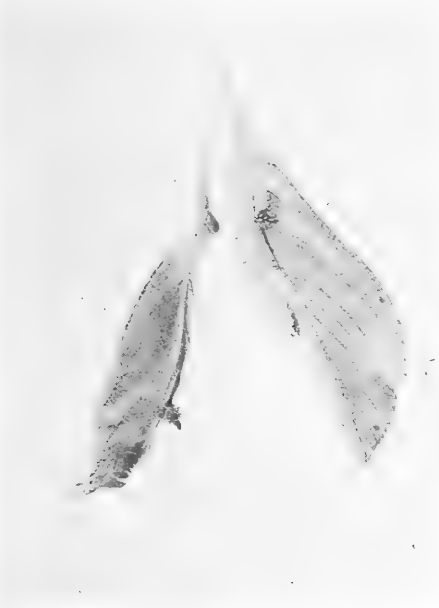


FIG. 122. PINEAPPLE GALLS

a long, narrow slit on the opposite side of the leaf. These galls occur very commonly in groups on the same leaf or on adjoining leaves. A single yellow larva, 1 millimeter long, and slender, is found in each gall in July or August.

Pineapple gall (maker unknown)

Red or green spiny galls, shaped and armored like a pineapple (figs. 122, 123, and 124), 3 millimeters in diameter and 5 millimeters high, are found on the upper side of *Crataegus punctata* leaves in July and August. The pineapple gall is thick and is covered with fleshy spines at the base, but becomes slender, with long, slender spines, toward the apex, which is composed of two flat, leaflike, vertical plates. The gall opens between these two plates. Generally but one gall is found on a leaf and it is commonly on the midvein.

Trypetidae

pomonella Walsh, *Rhagoletis* (Apple maggot)

The maggots of *Rhagoletis pomonella* have been reared and flies obtained from the fruits of *Crataegus punctata*, *C. albicans*, *C. pruinosa*, *C. brainerdi*, and *C. macrosperma*. The species probably lives also in the fruits of other large-fruited hawthorns. No larvae have been found in the small fruits of *C. neofluvialis* and *C. oxyacantha*, although these have been carefully watched. The maggots leave the fruit to enter the ground in autumn, and the flies emerge from the brown puparia in June and July.

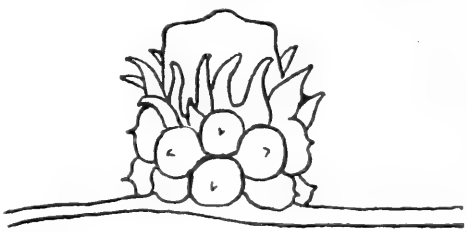


FIG. 123. SIDE VIEW OF PINEAPPLE GALL

All of the flies reared on hawthorns are equal in size to those reared on apple, not small like those reared on the blueberry. Counts were made of the infested and the uninfested fruits from a square yard beneath each of ten trees of the three species first mentioned in the preceding paragraph. The counts showed that from 20 to 25 per cent of the samples taken were infested by the maggots.

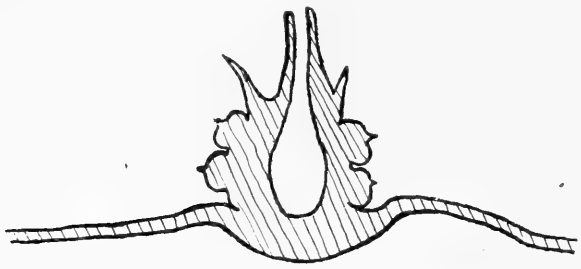


FIG. 124. CROSS SECTION THROUGH A PINEAPPLE GALL

HYMENOPTERA

Tenthredinidae

cerasi Linn., *Caliroa* (Pear and cherry slug)

The sluglike larvae of *Caliroa cerasi* were in a few localities so abundant that they defoliated a few native hawthorns and injured a number of others. In August, 1918, several trees on the Cornell University campus were completely defoliated, while neighboring trees were untouched by the larvae.

Sawfly No. 1

On June 23, 1918, a leaf of *Crataegus pruinosa* was found with a row of fourteen eggs inserted in the margin. The eggs hatched on June 28, and a row of little green larvae, with large, black heads and many black dots scattered over the body, began to feed gregariously on the edge of the leaf. All of them died within a few days.

Sawfly No 2

On May 24, 1918, several medium-sized sawfly larvae, bright green all over, were seen eating separately on the edges of *Crataegus punctata* leaves.

Sawfly No. 3

Sawfly larvae, with red heads and yellow bodies marked with black lines and dots, were found feeding on the leaves of *Crataegus punctata* in late August, 1918. They were feeding two or three together on a leaf, and fifteen larvae were taken from one tree. When they became about 2 centimeters long, on September 1 and 2, they spun brown cocoons on the ground among débris. A tree with ten larvae of the same species

feeding on it was found on September 19, 1919, and these larvae spun cocoons on the ground on September 22 and 23.

Sawfly No. 4

A few larvae $2\frac{1}{2}$ centimeters long, with black heads and yellow bodies marked with black lines and dots, were found feeding on the foliage of *C. pruinosa* in July and August, 1918. They spun brown cocoons on top of the ground, in the cages.

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HODGKISS, H. E. *Ceresa taurina* Fitch. *In* The apple and pear membracids. New York (Geneva) Agr. Exp. Sta. Tech. bul. 17:100–105. 1910.

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PIERCE, W. DWIGHT. The insect enemies of the cotton boll weevil. U. S. Ent. Bur. Bul. 100:1–99. 1912.

THEOBALD, FRED V. The app'e blossom weevil. *In* The insect and other allied pests of orchard, bush, and hothouse fruits, and their prevention and treatment, p. 104–110. 1909.

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Memoir 52, *Studies in Pollen, with Special Reference to Longevity*, the fourth preceding number in this series of publications, was mailed on March 9, 1922.

CATALOG OF INSECTS INJURIOUS TO CRATAEGUS[3]

ACARINA

armatus Can., *Epetrimerus*.....Fam. *Phyllocoptidae*
Host — *Crataegus oxyacantha.*
Injury — Forms galls on leaves.
Distribution — Europe.
References — Houard, C. Les zooececidès des plantes d'Europe, **1**:515. 1908.
Theobald, F. V. Board Agr. London. Journ. **20**:106–116. 1913.

calycobius Nal., *Eriophyes*.....Fam. *Eriophyidae*
Host — *Crataegus oxyacantha.*
Injury — Deforms leaf buds and causes them to remain closed.
Distribution — Europe.
Reference — Ross, H. Die Pflanzengallen Mittel- und Nordeuropas, p. 132. 1911.

crataegi Can., *Eriophyes*.....Fam. *Eriophyidae*
Host — *Crataegus oxyacantha.*
Injury — Forms galls on leaves, on both upper and lower surfaces. A single leaf may have a hundred galls on it.
Distribution — Europe.
Reference — Connold, E. T. British vegetable galls, p. 132. 1902.

crataegi-vermiculus Walsh, *Eriophyes*.....Fam. *Eriophyidae*
Hosts — *Crataegus tomentosa, C. crus-galli.*
Injury — Forms curled leaf galls on upper side of leaf.
Distribution — North America.
Reference — Walsh, B. D. Ent. Soc. Philadelphia. Proc. **6**:227. 1866.

goniothorax Nal., *Eriophyes*.....Fam. *Eriophyidae*
Synonyms — *Erineum oxyacanthae* Am., *Erineum clandestinum* Grev.
Host — *Crataegus oxyacantha.*
Injury — Forms galls on edges of lobes of leaf, causing them to curl downward and become thickened.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872.
Connold, E. T. British vegetable galls, p. 138. 1902.

pilosus Can., *Tetranychus*.....Fam. *Tetranychidae*
Hosts — Crataegus, Malus, Pyrus, Prunus.
Injury — Feeds on leaves, causing them to turn brownish.
Distribution — Europe, North America.
Reference — Caesar, L. Can. ent. **47**:57. 1915.

pyracanthae Link., *Eriophyes*.....Fam. *Eriophyidae*
Hosts — *Crataegus punctata, C. pyracantha.*
Injury — Makes galls on leaves. Galls almost flat, reddish, covered with many fine, capitate hairs.
Distribution — North America.
Reference — Chadwick, G. H. New York State Mus. Bul. 124:131. 1908.

pyri Pagst., *Eriophyes* (Pear leaf blister mite).....Fam. *Eriophyidae*
Hosts — Pyrus, Malus, Crataegus, Cydonia, Sorbus, Amelanchier.
Injury — Makes yellowish or reddish blisters on leaves.

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[3] The insects are grouped according to order, and arranged alphabetically by species within the order

Distribution — Europe, North America, Australia.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 227. 1914.
Wilson, H. F. Oregon Agr. Exp. Sta. Bien. crop pest and hort. rept. 2:123. 1915.

telarius Linn., *Tetranychus* (Red spider) ..... Fam. *Tetranychidae*
(See page 1051.)

Eriophyes sp. (Hawthorn serpentine gall of Jarvis) ..... Fam. *Eriophyidae*
Host — Crataegus.
Injury — Makes long, irregular, wavy galls on upper surface of leaves.
Distribution — North America.
Reference — Jarvis, T. D. Ent. Soc. Ont. Rept. 37:60. 1906.
(Figs. 102 and 103, pages 1052 and 1053.)

ORTHOPTERA

atlanis Riley, *Melanoplus* ..... Fam. *Acridiidae*
(See page 1054.)

bivitattus Say, *Melanoplus* ..... Fam. *Acridiidae*
(See page 1054.)

femur-rubrum De Geer, *Melanoplus* ..... Fam. *Acridiidae*
(See page 1054.)

niveus De Geer, *Oecanthus* (Snowy tree cricket) ..... Fam. *Gryllidae*
Hosts — Malus, Rubus, Salix, Crataegus, Ulmus, Quercus, and other species.
Injury — Female slits bark to deposit eggs. Slits give entrance to cankers and cause scars on branches.
Distribution — North America, Cuba.
Reference — Parrott, P. J., and Fulton, B. B. New York (Geneva) Agr. Exp. Sta. Bul. 388. 1914.

ODONATA

viridis v. d. Lind., *Lestes* ..... Fam. *Agrionidae*
Hosts — *Crataegus oxyacantha* and other species.
Injury — Oviposition punctures in twigs cause galls to form.
Distribution — Europe.
References — Pierre, P. F. M. Rev. sci. Bourbonnais 15:181. 1902.
Houard, C. Les zoocecides des plantes d'Europe, 1:514. 1908.

HEMIPTERA

aceris Sign., *Phenacoccus* ..... Fam. *Coccidae*
Hosts — *Crataegus oxyacantha* and many other woody plants.
Injury — Sucks sap from tender bark of young shoots and calloused wounds. Sometimes seriously injures grape.
Distribution — Europe.
References — Lindinger, L. Die Schildläuse, p. 214. 1912.
Carpenter, G. H. Roy. Dublin Soc. Econ. proc. 2:142–160. 1914.

ambiguus Fall., *Psallus* ..... Fam. *Miridae*
Hosts — Crataegus, Pyrus, Malus, Alnetis.
Distribution — Europe.
References — Reuter, O. M. Hemiptera gymnocerata Europae 1:105. 1878.
Leonardi, G. Gli insetti 4:98. 1901.

bakeri Cowen, *Aphis* (Clover aphid) ..... Fam. *Aphididae*
Hosts — Malus, Crataegus, clover.
Injury — Sucks juice from opening buds of fruit trees.
Distribution — North America.
References — Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804:15. 1917.
Patch, E. M. Maine Agr. Exp. Sta. Bul. 270:49. 1918.

bellula Gibson, *Corythucha* ..... Fam. *Tingitidae*
Hosts — *Crataegus neofluvialis, C. punctata, C. albicans, Alnus incana, Ribes oxyacanthoides.*
Injury — Both young and adult bugs suck juice from leaves, causing them to turn brown and drop off.
Distribution — Northeastern United States, Canada.
References — Gibson, E. H. Amer. Ent. Soc. Trans. 44:93. 1918.
Wellhouse, W. H. Journ. econ. ent. 12:441. 1919.
(Plates LXXII and LXXIII, pages 1057 and 1059.)

betulae Bär., *Epidiaspis* (European pear scale) ..... Fam. *Coccidae*
Synonyms — *Epidiaspis leperi* Sign., *E. piricola* De Geer, *Diaspis piri* Colv.
Hosts — Pyrus, Malus, Prunus, Crataegus, and other species.
Injury — Very injurious to young twigs and branches of apple and pear in southern Europe, where the bark becomes incrusted.
Distribution — South and middle Europe, United States.
References — Lindinger, L. Die Schildläuse, p. 213. 1912.
Essig, E. O. Injurious and beneficial insects of California, p. 172. 1915.

bituberculatum Targ., *Lecanium* ..... Fam. *Coccidae*
Hosts — *Crataegus oxyacantha*, Malus, Pyrus.
Injury — Sucks sap from bark, sometimes killing young trees.
Distribution — Europe, North America.
References — Sorauer, P. Handbuch der Pflanzenkrankheiten 3:695. 1913.
Dietz, H. F., and Morrison, H. Indiana State Ent. Ann. rept. 8:254. 1916.

brevis Sand., *Aphis* (Long-beaked clover aphid) ..... Fam. *Aphididae*
Hosts — Crataegus, Cydonia, Pyrus, clovers, sweet pea.
Injury — Curls and turns purplish the terminal leaves of Crataegus shoots during June.
Distribution — United States.
Reference — Patch, E. M. Journ. agr. res. 3:431. 1915.

brunnea Gibson, *Corythucha* ..... Fam. *Tingitidae*
Host — Crataegus.
Injury — Sucks juice from foliage.
Distribution — Southern United States.
Reference — Gibson, E. H. Amer. Ent. Soc. Trans. 44:93. 1918.

bubalis Fabr., *Ceresa* (Buffalo tree hopper) ..... Fam. *Membracidae*
Hosts — Malus, Crataegus, and other species.
Injury — Adult makes incisions in branches for oviposition. Incisions are slow to heal and allow entrance of borers and fungi.
Distribution — North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 535. 1890.
Hodgkiss, H. E. New York (Geneva) Agr. Exp. Sta. Tech. bul. 17:92. 1910.

clitellarius Say, *Thamnotettix* ..... Fam. *Cicadellidae*
(See page 1061.)

coccinea Först., *Graphocephala*.....Fam. *Cicadellidae*
(See page 1061.)

communis Knight, *Lygus*.....Fam. *Miridae*
(See page 1054.)

corni Bouché, *Lecanium* (European fruit lecanium).....Fam. *Coccidae*
Hosts — Crataegus, Malus, Prunus, and other species.
Injury — May suck so much sap from branches as to kill them, but commoner injury is due to growth of sooty fungus over sticky secretion which the insects drop on foliage, fruit, and branches.
Distribution — Europe, North America.
References — Sorauer, P. Handbuch der Pflanzenkrankheiten **3**:695. 1913.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 261. 1914.

corrugatans Sir., *Pemphigus* (Woolly thorn aphis).....Fam. *Aphididae*
Hosts — Crataegus, Amelanchier, Pyrus, Cydonia.
Injury — Distorts leaves into a rolled curl.
Distribution — North America.
References — Patch, E. M. Maine Agr. Exp. Sta. Bul. 233. 1914.
Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804:19. 1917.

coryli Linn., *Lecanium*.....Fam. *Coccidae*
Synonyms — *Eulecanium pyri* Schr., *Lecanium capreae* Linn.
Hosts — Malus, Crataegus, Pyrus, and other species.
Injury — Sucks sap from bark, not commonly injurious.
Distribution — Europe, North America.
References — Theobald, F. V. Insect pests of fruits, p. 175. 1909.
Lindinger, L. Die Schildläuse, p. 216. 1912.

costalis Flor., *Psylla*.....Fam. *Psyllidae*
Hosts — Malus, Crataegus, Sorbus, Quercus.
Distribution — Europe.
Refere ce — Harrison, J. W. H. Naturalist (London), no. 707, p. 400. 1915.

crataegarium Walk., *Macrosiphum*.....Fam. *Aphididae*
Host — *Crataegus oxyacantha*.
Distribution — Enlgand.
References — Walker, F. Ann. mag. nat. hist. **6**:46. 1850.
Theobald, F. V. Journ. econ. biol. 8:142. 1913.

crataegi Kalt., *Aphis*.....Fam. *Aphididae*
Synonyms — *Aphis pyri* Boyer, *A. crataegi* Koch, *A. ranunculi* Kalt.
Hosts — *Crataegus oxyacantha, C. azarolus*, Malus, Ranunculus.
Injury — Curls, discolors, and blisters leaves on terminal shoots.
Distribution — Europe.
References — Dobrovliansky, V. V. Biology of aphids of tree and bush fruits (Kiev). 1913.
Van der Goot, P. Holländischen Blattläuse, p. 174. 1915.
Theobald, F. V. Entomologist 48:259. 1915.

crataegi Fitch, *Glossonotus* (Hawthorn tree hopper).....Fam. *Membracidae*
Hosts — Crataegus, Malus, Cydonia.
Distribution — North America.
References — Fitch, A. Third annual report on noxious insects of New York, p. 334. 1856.
Funkhouser, W. D. Cornell Univ. Agr. Exp. Sta. Memoir 11:248. 1917.

crataegi VanD., *Idiocerus*.....Fam. *Cicadellidae*
Host — Crataegus.
Injury — Adults and young suck juice from foliage.
Distribution — North America.
Reference — Van Duzee, E. P. Can. ent. **22**:110. 1890.

crataegi Monell, *Macrosiphum*.....Fam. *Aphididae*
Hosts — *Crataegus punctata, C. coccinea, C. oxyacantha.*
Injury — Sucks juice from lower side of leaves and from tender twigs. Leaves curl downward and in severe infestations trees may be defoliated.
Distribution — North America.
Reference — Patch, E. M. Maine Agr. Exp. Sta. Bul. 233:255. 1914. (Fig. 108, page 1063.)

crataegi Tullgr., *Prociphilus*.....Fam. *Aphididae*
Hosts — *Crataegus oxyacantha*, Malus.
Injury — Curls and discolors leaves and sometimes injures blossoms.
Distribution — Europe.
Reference — Van der Goot, P. Holländischen Blattläuse, p. 450. 1915.

crataegi Schr., *Psylla*.....Fam. *Psyllidae*
Synonym — *Chermes quercus* Thoms.
Hosts — *Crataegus oxyacantha, Quercus* sp.
Injury — Causes small red blisters to form on upper side of leaves.
Distribution — Europe.
Reference — Aulmann, G. Psyllidarum catalogus, p. 13. 1913.

crataegi Dgl., *Typhlocyba*.....Fam. *Cicadellidae*
Hosts — *Crataegus oxyacantha*, apple (?).
Injury — Nymphs and adults suck juice from foliage, but commonly they are not numerous enough to cause much injury.
Distribution — Europe.
References — Douglas, J. W. Ent. mo. mag. **12**:203. 1876.
Melichar, L. Cicadinen von Mittel-Europe, p. 348. 1896.

crataegiella Theobald, *Aphis*.....Fam. *Aphididae*
Synonym — *Aphis crataegi* Buck.
Host — *Crataegus oxyacantha.*
Injury — Curls and discolors leaves of terminal shoots, which turn reddish brown.
Distribution — Europe.
References — Buckton, G. B. Monograph of British aphides, **2**:35. 1879.
Theobald, F. V. List of Aphididae of Hastings District, p. 9. 1912.

crataegifoliae Fitch, *Aphis*.....Fam. *Aphididae*
Hosts — *Crataegus punctata, C. coccinea, C. oxyacantha, C. tomentosa,* Cydonia, legumes.
Injury — Curls and discolors leaves and young shoots, turning them purplish.
Distribution — North America.
Reference — Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804:18. 1917.

crataegus-coccinea Rafin., *Aphis*.....Fam. *Aphididae*
Host — *Crataegus coccinea.*
Distribution — North America.
References — Rafinesque, C. S. Amer. mo. mag. and crit. rev. **3**:16. 1818.
Patch, E. M. Maine Agr. Exp. Sta. Bul. 270:48. 1918.

curtisii Fb., *Euscelis*.....Fam. *Cicadellidae*
(See page 1161.)

cydoniae Fitch, *Corythucha*.....Fam. *Tingitidae*
Synonyms — *Corythucha arcuata* Comst., *C. crataegi* O. & D.
Hosts — Crataegus, Cydonia.
Injury — Nymphs and adults suck juice from leaves, causing them to turn brown.
Distribution — North America.
References — Fitch, A. Country gent. **17**:25. 1861.
Comstock, J. H. U. S. Ent. Rept. **1879**:221. 1879.
Gibson, E. H. Amer. Ent. Soc. Trans. **44**:87. 1918.

dearnessi King, *Phenacoccus*.....Fam. *Coccidae*
Synonym — *Phenacoccus betheli* Ckll.
Hosts — Crataegus, Amelanchier.
Distribution — Canada, United States.
Reference — Ferris, G. F. Contribution to knowledge of Coccidae of southwestern United States, p. 68. 1919.

dislocatus Say, *Horcias*.....Fam. *Miridae*
(See page 1054.)

dumetorum Schiff., *Physatocheila*.....Fam. *Tingitidae*
Hosts — *Crataegus oxyacantha, Pyrus communis, Prunus padus, P. spinosa.*
Distribution — Europe, Egypt.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872.
Saunders, E. Hemiptera of British Islands, p. 135. 1892.

edentula Buck., *Aphis*.....Fam. *Aphididae*
Host — *Crataegus oxyacantha.*
Distribution — Europe.
Reference — Buckton, G. B. Monograph of British aphides, **2**:39. 1879.

fitchi VanD., *Idiocerus* (Black apple leaf hopper).....Fam. *Cicadellidae*
Synonym — *Idiocerus maculipennis* Fitch.
Hosts — Crataegus, Malus, Pyrus.
Injury — Adults and young suck juice from foliage. Not commonly injurious.
Distribution — North America.
References — Van Duzee, E. P. Catalog of Hemiptera, p. 580. 1916.
Brittain, W. H., and Saunders, L. G. Can. ent. **49**:149. 1917.

flavicephala Goding, *Ophiderma*.....Fam. *Membracidae*
(See page 1063.)

furfura Fitch, *Chionaspis* (Scurfy scale).....Fam. *Coccidae*
Hosts — About 25 tree species, including Crataegus, Malus, Pyrus, Cydonia, Sorbus.
Injury — Occasionally incrusts bark of trees and greatly weakens or kills them.
Distribution — North America.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 176. 1914.
Essig, E. O. Injurious and beneficial insects of California, p. 158. 1915.

hederae Vall., *Aspidiotus*.....Fam. *Coccidae*
Synonym — *Aspidiotus nerii* Bouché.
Hosts — Many woody and herbaceous plants, including *Crataegus azarolus.*
Distribution — Europe, Asia, North Africa (on Crataegus in Algeria), North America.
References — Lindinger, L. Die Schildläuse, p. 213. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten **3**:689. 1913.

lachrymalis Fb., *Idiocerus*.....Fam. *Cicadellidae*
(See page 1061.)

lanigera Hausm., *Eriosoma* (Woolly aphis) ..... Fam. *Aphididae*
Synonyms — *Eriosoma crataegi* Oest., *Schizoneura americana* Riley.
Hosts — Crataegus, Malus, *Ulmus americana.*
Injury — Sucks sap from tender shoots, branches, and roots, often stunting growth.
Distribution — North America, Europe, Africa, Australia, South America.
References — Theobald, F. V. Insect pests of fruits, p. 141. 1909.
Baker, A. C. U. S. Agr. Dept. Rept. **101**. 1915.
Becker, G. G. Journ. econ. ent. **11**:245. 1918.
(Fig. 109, page 1064.)

lineatus Linn., *Philaenus* ..... Fam. *Cicadellidae*
(See page 1061.)

mali LeB., *Empoasca* (Apple leaf hopper) ..... Fam. *Cicadellidae*
(See page 1061.)

mali Schmid., *Psylla* ..... Fam. *Psyllidae*
Synonym — *Psylla crataegicola* Först.
Hosts — *Crataegus oxyacantha*, Malus, Pyrus, Sorbus, Quercus, Ulmus, Corylus.
Injury — Nymphs suck juice from foliage and blossoms, and prevent setting of fruit.
Distribution — Europe, Asia, Nova Scotia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872.
Theobald, F. V. Insect pests of fruits, p. 153. 1909.
Brittain, W. H. Journ. econ. ent. **15**:96. 1922.

malinus Reuter, *Heterocordylus* (Dark apple redbug) ..... Fam. *Miridae*
Hosts — Crataegus, Malus.
Injury — Nymphs and adults puncture leaves and fruit to suck juice. Cause dimples in fruit, which deform it.
Distribution — Northeastern United States, Canada.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 28. 1914.
Cushman, R. A. Ent. Soc. Washington. Proc. **18**:196. 1916.

marutae Oest., *Aphis* ..... Fam. *Aphididae*
Hosts — Crataegus, *Anthemis cotula.*
Distribution — North America.
References — Oestlund, O. W. Aphididae of Minnesota, p. 40. 1886.
Hunter, 1901, p. 101. (*Cited by* Patch, E. M. Maine Agr. Exp. Sta. Bul. 270:49. 1918.)

melanoneura Först., *Psylla* ..... Fam. *Psyllidae*
Synonym — *Psylla crataegi* Först.
Hosts — *Crataegus oxyacantha*, Quercus, and other species.
Distribution — Europe, Asia.
References — Aulmann, G. Psyllidarum catalogus, p. 20. 1913.
Harrison, J. W. H. Naturalist (London), no. 707, p. 400. 1915.

mendax Reuter, *Lygidea* (Bright apple redbug) ..... Fam. *Miridae*
Hosts — Malus, Crataegus.
Injury — Nymphs and adults puncture leaves and fruit to suck juice, and cause dimples in fruit.
Distribution — Northeastern United States, Canada.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 28. 1914.
Cushman, R. A. Ent. Soc. Washington. Proc. **18**:196. 1916.

mespili v.d.G., *Ovatus* ..... Fam. *Aphididae*
Hosts — *Crataegus oxyacantha, Mespilus germanica.*

Injury — Sucks sap from tender shoots and leaves.
Distribution — Europe.
Reference — Van der Goot, P. Holländischen Blattläuse, p. 136. 1915.

nigrofasciatum Perg., *Lecanium* (Terrapin scale) ..... Fam. *Coccidae*
Hosts — Prunus, Acer, Malus, Crataegus, Tilia, Platanus, and other species.
Injury — Sucks sap from bark and secretes much sticky liquid, which covers surface of branches, foliage, and fruit and on which a sooty fungus grows, thus rendering fruit unsalable.
Distribution — North America.
References — Felt, E.P. New York State Mus. Memoir 8[1]:201. 1905.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 293. 1914.

obliqua Say, *Erythroneura* ..... Fam. *Cicadellidae*
(See page 1061.)

oleae Colvee, *Parlatoria* ..... Fam. *Coccidae*
Hosts — Many woody plants, including *Crataegus germanica*.
Injury — May incrust the bark, and sometimes the leaves and the fruit, of trees of the genera Citrus, Pyrus, and Olea especially.
Distribution — Mediterranean region.
References — Lindinger, L. Die Schildläuse, p. 213. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten **3**:694. 1913.

olivaceus Fabr., *Deraeocoris* ..... Fam. *Miridae*
Synonym — *Capsus medius* Kirschb.
Hosts — Malus, Crataegus, Prunus, Corylus.
Injury — Sucks juice from foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872.
Reuter, O. M. Hemiptera gymnocerata Europae **5**:30. 1896.

ornatus VanD., *Orthotylus* ..... Fam. *Miridae*
(See page 1055.)

ostreiformis Curt., *Aspidiotus* (European fruit-tree scale) ..... Fam. *Coccidae*
Synonym — *Aspidiotus oxyacanthae* Sign.
Hosts — Malus, Prunus, Pyrus, Crataegus, and many other woody plants.
Injury — May completely incrust the bark and kill the tree.
Distribution — Europe, Asia Minor, North America.
References — Theobald, F. V. Insect pests of fruits, p. 386. 1909.
Lindinger, L. Die Schildläuse, p. 213. 1912.

ostryae Knight, *Lygus* ..... Fam. *Miridae*
(See page 1055.)

oxyacanthae Schr., *Myzus* ..... Fam. *Aphididae*
Synonym — *Aphis oxyacanthae* Koch.
Hosts — *Crataegus oxyacantha*, Pyrus, Malus, Prunus.
Injury — Sucks juice from leaves, causing yellow or red swellings on them and making them curl.
Distribution — Europe.
References — Koch, C. L. Pflanzenläuse, p. 55. 1857.
Ross, H. Die Pflanzengallen Mittel- und Nordeuropas, p. 132. 1911.

padi Linn., *Rhopalosiphum* ..... Fam. *Aphididae*
Synonyms — *Aphis avenae* Fabr., *Aphis padi* Kalt.
Hosts — *Prunus padus*, Crataegus, Malus, Pyrus, grasses.

Injury — Sucks juice from opening buds of fruit trees in early spring.
Distribution — Europe, North America.
References — Leonardi, G. Gli insetti 4:228. 1901.
Baker, A. C. Journ. agr. res. 18:311. 1919.

pallidus Fb., *Idiocerus*.....Fam. *Cicadellidae*
(See page 1062.)

pellucida Uhl., *Diaphnidia*.....Fam. *Miridae*
(See page 1055.)

peregrina Först., *Psylla*.....Fam. *Psyllidae*
Synonym — *Psylla crataegicola* Flor.
Hosts — *Crataegus oxyacantha, Carpinus betulus.*
Injury — Sucks juice from young shoots and foliage.
Distribution — Europe, Asia.
Reference — Aulmann, G. Psyllidarum catalogus, p. 22. 1913.

perniciosus Comst., *Aspidiotus* (San José scale).....Fam. *Coccidae*
Hosts — Many woody plants, including Crataegus and other Malaceae.
Injury — May incrust bark and kill trees in favorable weather.
Distribution — Asia, North America, South America, Australia, Hawaii.
References — Sorauer, P. Handbuch der Pflanzenkrankheiten 3:690. 1913.
Glenn, P. A. State Ent. Illinois. Rept. 28:87. 1915.

piri Licht., *Aspidiotus*.....Fam. *Coccidae*
Hosts — Pyrus, Malus, Crataegus, Fraxinus, Prunus.
Injury— May incrust branches and thus weaken or kill them.
Distribution — Europe, Asia Minor.
References — Lindinger, L. Die Schildläuse, p. 214. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3:690. 1913.

pomi De Geer, *Aphis* (Green apple aphis).....Fam. *Aphididae*
Synonyms — *Aphis mali* Fabr., *A. oxyacanthae* Schr.
Hosts — Malus, Crataegus, grasses.
Injury — Sucks sap, causing leaves to curl, but no discoloration appears.
Distribution — Europe, North America.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 202. 1872.
Matheson, R. Cornell Univ. Agr. Exp. Sta. Memoir 24:686. 1919.

pratensis Linn., *Lygus*.....Fam. *Miridae*
(See page 1055.)

provancheri VanD., *Idiocerus*.....Fam. *Cicadellidae*
Hosts — Crataegus, Malus, Pyrus, Cydonia.
Injury — Nymphs and adults suck juice from foliage.
Distribution — North America.
References — Leonard, M. D. Journ. econ. ent. 8:415. 1915.
Van Duzee, E. P. Catalog of Hemiptera, p. 580. 1916.

pruinosum Coq., *Lecanium* (Frosted scale).....Fam. *Coccidae*
Hosts — Many woody plants, including Crataegus.
Injury — Principal injury from smutty fungus growing on honeydew secreted by insects on fruit and foliage.
Distribution — North America.
References — Sanders, J. G. Journ. econ. ent. 2:442. 1909.
Essig, E. O. Injurious and beneficial insects of California, p. 149. 1915.

prunifoliae Fitch, *Rhopalosiphum* (Apple bud aphis).....Fam. *Aphididae*
Synonyms — *Aphis avenae* (of American authors), *Aphis fitchii* Sand.

Hosts — Malus, Pyrus, Crataegus, Prunus, many grasses.
Injury — Sucks juice from opening buds of trees in spring.
Distribution — North America.
References — Quaintance, A. L. U. S. Ent. Bur. Circ. 81. 1907.
Baker, A. C. Journ. agr. res. 18:311. 1919.

pumilus Uhl., *Cerctocapsus*.....Fam. *Miridae*
Synonym — *Melinna pumila* Uhl.
Hosts — Crataegus, Salix.
Injury — Adult sucks sap from foliage.
Distribution — Eastern United States.
Reference — Uhler, P. R. Ent. Amer. 3:69. 1887.

pyri Fitch, *Prociphilus* (Pear root aphis).....Fam. *Aphididae*
Hosts — Pyrus, Crataegus, Malus.
Injury — Sucks sap from roots.
Distribution — Eastern North America.
References — Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804:19. 1917.
Wilson, H. F., and Vickery, R. A. Wisconsin Acad. Sci., Arts, and Letters. Trans. 19:140. 1918.

querci Fitch, *Empoa*.....Fam. *Cicadellidae*
(See page 1032.)

rosae Linn., *Empoa* (Rose leaf hopper).....Fam. *Cicadellidae*
Hosts — Rosa, Malus, Pyrus, Prunus, Crataegus, Cydonia, and other species.
Injury — Nymphs and adults suck juice from lower leaves of trees, causing yellowing of foliage and in some cases defoliation.
Distribution — Europe, North America.
Reference — Ackerman, A. J. U. S. Agr. Dept. Bul. 805:20. 1919.

rumicis Linn., *Aphis*.....Fam. *Aphididae*
Hosts — Many herbs and woody plants, including *Crataegus oxyacantha* and pear.
Injury — Sucks juice from foliage in spring and fall.
Distribution — Europe, North America.
References — Börner. Nat. Ver. Bremen. Abhandl. 23:152. 1914.
Van der Goot, P. Holländischen Blattläuse, p. 220. 1915.

rusci Linn., *Ceroplastes*.....Fam. *Coccidae*
Hosts — Many plants, including Crataegus.
Injury — Sucks juice from bark, leaves, and fruit.
Distribution — Mediterranean region.
References — Lindinger, L. Die Schildläuse, p. 214. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3:695. 1913.

saliceti Först., *Psylla*.....Fam. *Psyllidae*
Hosts — Salix, *Crataegus oxyacantha*.
Injury — Sucks juice from foliage.
Distribution — Europe, Asia, Japan.
Reference — Aulmann, G. Psyllidarum catalogus, p. 26. 1913.

seminudus Say, *Eutettix*.....Fam. *Cicadellidae*
(See page 1062.)

sorbi Kalt., *Aphis* (Rosy apple aphis).....Fam. *Aphididae*
Synonym — *Aphis malifoliae* Fitch.
Hosts — Malus, Pyrus, Crataegus, Sorbus, Plantago.
Injury — Curls leaves and deforms fruit.

Distribution — Europe, North America.
References — Van der Goot, P. Holländischen Blattläuse, p. 177. 1915.
Matheson, R. Cornell Univ. Agr. Exp. Sta. Memoir 24:718. 1919.

suturalis Fb., *Idiocerus*.....Fam. *Cicadellidae*
(See page 1062.)

taurina Fitch, *Ceresa*.....Fam. *Membracidae*
(See page 1063.)

ulmi Linn., *Lepidosaphes* (Oyster-shell scale).....Fam. *Coccidae*
Synonym — *Mytilaspis pomorum* Bouché.
Hosts — Many woody plants, including Crataegus.
Injury — Sucks juice from bark and foliage.
Distribution — Europe, Asia, Africa, Australia, North America, South America, Hawaii.
References — Theobald, F. V. Insect pests of fruits, p. 170. 1909.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3:692. 1913.

ulmi Geof., *Tetraneura*.....Fam. *Aphididae*
Hosts — Ulmus, *Crataegus oxyacantha*, many grasses.
Injury — Sucks juice from leaves, causing galls to form on upper surface.
Distribution — Europe.
References — Van der Goot, P. Holländischen Blattläuse, p. 484. 1915.
Patch, E. M. Maine Agr. Exp. Sta. Bul. 270:49. 1918.

univittatus Knight, *Lygus*.....Fam. *Miridae*
Host — Crataegus.
Injury — Adults suck juice and puncture fruit and tender foliage.
Distribution — Northeastern United States.
Reference — Knight, H. H. Brooklyn Ent. Soc. Bul. 14:21. 1919.

urticae Linn., *Trioza*.....Fam. *Psyllidae*
Hosts — Urtica, *Crataegus oxyacantha*.
Injury — Sucks juice from foliage.
Distribution — Europe, Asia.
References — Aulmann, G. Psyllidarum catalogus, p. 56. 1913.
Harrison, J. W. H. Naturalist (London), no. 707, p. 400. 1915.

vanduzei Gill., *Eupteryx*.....Fam. *Cicadellidae*
(See page 1062.)

vitis Linn., *Pulvinaria* (Cottony scale).....Fam. *Coccidae*
Synonyms — *Pulvinaria betulae* Linn., *P. innumerabilis* Rath., *P. oxyacanthae* Linn.
Hosts — Many woody plants, including Crataegus.
Injury — Sucks sap from bark and tender shoots.
Distribution — Europe, America, Africa, Asia Minor.
Reference — Lindinger, L. Die Schildläuse, p. 215. 1912.

vulgaris Fb., *Lamenia*.....Fam. *Cicadellidae*
(See page 1063.)

THYSANOPTERA

tritici Fitch, *Euthrips*.....Fam. *Thrypidae*
(See page 1066.)

COLEOPTERA

aeneovirens Marsh, *Rhynchites*, var. *punctatus* Oliv.....Fam. *Curculionidae*
Host — *Crataegus oxyacantha*.
Distribution — Europe.
Reference — Bargagli, P. Rincofori Europei, p. 181. 1883.

aenescens Lec., *Magdalis* (Bronze apple weevil) ..... Fam. *Curculionidae*
Hosts — Malus, Crataegus, Prunus.
Injury — Larva tunnels under bark, sometimes killing tree. Adults feed on leaves.
Distribution — Northwestern United States, Canada.
References — Chittenden, F. H. U. S. Ent. Bur. Bul. 22:37. 1900.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 199. 1914.

aequatus Linn., *Rhynchites* ..... Fam. *Curculionidae*
Hosts — Crataegus, Malus, Prunus, Sorbus.
Injury — Beetles puncture fruit buds and leaves in feeding.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 181. 1872.
Bargagli, P. Rincofori Europei, p. 181. 1883.

aerosus Melsh., *Brachys* ..... Fam. *Buprestidae*
(See page 1066.)

albida Lec., *Syneta* ..... Fam. *Chrysomelidae*
Hosts — Malus, Pyrus, Cydonia, Crataegus, Prunus, Corylus, and other species.
Injury — Beetles feed on flowers and foliage, sometimes defoliating young trees.
Distribution — Western United States.
References — Wilson, H. F., and Moznette, G. F. Oregon Agr. Exp. Sta. Bien. crop pest and hort. rept. 2:96. 1915.

alpina Linn., *Rosalia* ..... Fam. *Cerambycidae*
Hosts — *Crataegus oxyacantha*, *Fagus* sp.
Injury — Larva tunnels under bark, girdling branches, and then enters solid wood.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Holeczek, A. Ent. Nachr. 13:308. 1887.

auratus Scop., *Rhynchites* ..... Fam. *Curculionidae*
Synonym — *Rhynchites bacchus* Oliv.
Hosts — *Crataegus oxyacantha*, *Prunus spinosa*, Malus.
Injury — Beetles cut off petioles of leaves, and larvae feed in fruit.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 153. 1872.
Bargagli, P. Rincofori Europei, p. 183. 1883.

bacchus Linn., *Rhynchites* (Purple apple weevil) ..... Fam. *Curculionidae*
Hosts — Malus, Crataegus.
Injury — Larvae feed in fruit, much like codling moth.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Theobald, F. V. Insect pests of fruits, p. 121. 1909.

barbicornis Lat., *Magdalis* (Apple stem piercer) ..... Fam. *Curculionidae*
Hosts — Malus, Cydonia, Crataegus.
Injury — Larvae tunnel under bark, causing discolored, sunken areas.
Distribution — Europe, United States (New York and Massachusetts), imported recently.
References — Henschel, G. A. O. Die schädlichen forst- und obstbaum Insekten, p. 94. 1895.
Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 257. 1916.
Pierce, W. D. Manual of dangerous insects, p. 132. 1917.

bipunctatus Linn., *Cryptocephalus* ..... Fam. *Chrysomelidae*
Hosts — Crataegus, Corylus, Salix, Betula.

Injury — Beetles eat holes in foliage.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Käfer, p. 901. 1858.
Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.

borealis Shev., *Dibolia*.....Fam. *Chrysomelidae*
(See page 1067.)

calva Lec., *Limnobaris*.....Fam. *Curculionidae*
Host — Crataegus.
Distribution — Eastern United States.
Reference — Hamilton, J. Amer. Ent. Soc. Trans. **22**:377. 1895.

candida Fabr., *Saperda* (Round-headed apple-tree borer).....Fam. *Cerambycidae*
Synonym — *Saperda bivittata* Say.
Hosts — Cydonia, Malus, Sorbus, Amelanchier, Pyrus, Crataegus.
Injury — Larvae tunnel under bark of trunk and into sapwood. Not commonly injurious to Crataegus.
Distribution — North America.
References — Glover, T. Manuscript notes from my journal, p. 87. 1877.
Felt, E. P., and Joutel, L. H. New York State Mus. Bul. 74:28. 1904.
Becker, G. G. Arkansas Agr. Exp. Sta. Bul. 146:5. 1918.

carinata Germ., *Haltica*.....Fam. *Chrysomelidae*
(See page 1067.)

caudatus Rossi, *Otiorrhynchus*.....Fam. *Curculionidae*
Host — *Crataegus oxyacantha*.
Distribution — Europe.
References — Marseul, M. S. A. Monographie des Otiorhynchides, p. 127. 1872.
Bargagli, P. Rincofori Europei, p. 63. 1883.

cerasi Linn., *Magdalis*.....Fam. *Curculionidae*
Hosts — *Prunus cerasus*, *P. padus*, *Crataegus oxyacantha*.
Injury — Larva burrows under bark.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Käfer, p. 758. 1858.
Bargagli, P. Rincofori Europei, p. 195. 1883.
Pierce, W. D. Manual of dangerous insects, p. 132. 1917.

coeruleocephalus Schel., *Rhynchites*.....Fam. *Curculionidae*
Hosts — *Crataegus oxyacantha*, Betula, Quercus.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 589. 1872.
Bargagli, P. Rincofori Europei, p. 187. 1883.

colaspidoides Gyll., *Diphucephala*.....Fam. *Scarabaeidae*
Hosts — Prunus, *Crataegus oxyacantha*.
Injury — Beetles appear in swarms, like locusts, and defoliate trees and shrubs.
Distribution — Australia.
References — Insect life **3**:425. 1890.
French, C. Destructive insects of Victoria, **2**:27. 1893.

convergeus Lec., *Xylotrechus*.....Fam. *Cerambycidae*
Host — *Crataegus* sp.
Injury — Larva tunnels in branches.
Distribution — North America.
Reference — LeConte, J. L. Amer. Ent. Soc. Trans. 8:xxiv. 1880.

crataegi Walsh, *Conotrachelus* (Quince curculio) ..... Fam. *Curculionidae*
Hosts — *Crataegus* spp., Cydonia.
Injury — Larvae feed within fruit, partially destroying it.
Distribution — Eastern United States.
References — Riley, C. V. Third Missouri rept., p. 35. 1871.
Slingerland, M. V. Cornell Univ. Agr. Exp. Sta. Bul. 148. 1898.

crataegi Germ., *Otiorrhynchus* ..... Fam. *Curculionidae*
Host — *Crataegus oxyacantha.*
Distribution — Europe.
References — Marseul, M. S. A. Monographie des Otiorhynchides, p. 287. 1872.
Bargagli, P. Rincofori Europei, p. 63. 1883.

crataegi Walsh, *Pseudanthonomus* (Apple weevil) ..... Fam. *Curculionidae*
Hosts — Crataegus, Malus, *Kalmia latifolia.*
Injury — Larvae burrow in fruit, beetles puncture fruit and foliage.
Distribution — Eastern United States, Canada.
References — Brooks, F. E. West Virginia Agr. Exp. Sta. Bul. 126. 1910.
Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 318. 1916.

cretata Newm., *Saperda* (Spotted apple-tree borer) ..... Fam. *Cerambycidae*
Hosts — Malus, Crataegus, Amelanchier.
Injury — Larvae kill branches by girdling and tunneling in sapwood.
Distribution — Eastern North America.
References — Osborn, H. Iowa State Hort. Soc. Trans. **15**:11. 1880.
Hamilton, J. Amer. Ent. Soc. Trans. **22**:369. 1895.
Felt, E. P., and Joutel, L. H. New York State Mus. Bul. 74:50. 1904.

cucumeris Harris, *Epitrix* ..... Fam. *Chrysomelidae*
(See page 1067.)

decipiens Lec., *Anthonomus* ..... Fam. *Curculionidae*
Hosts — Crataegus, cotton (?); beetles in abundance beaten from *Crataegus* sp. by Dr. Hamilton.
Distribution — North America.
Reference — Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 316. 1916.

dorsalis Thunb., *Chalepus* ..... Fam. *Chrysomelidae*
Hosts — Robinia, Malus, Quercus, Crataegus, Rubus, and other species.
Injury — Beetles eat foliage.
Distribution — North America.
Reference — Houser, J. S. Ohio Agr. Exp. Sta. Bul. 332:231. 1918.

dubitans Lec., *Limonius* ..... Fam. *Elateridae*
(See page 1066.)

elongata Fabr., *Dichelonycha* ..... Fam. *Scarabaeidae*
(See page 1066.)

fayi Bland, *Saperda* (Thorn limb borer) ..... Fam. *Cerambycidae*
Hosts — *Crataegus crus-galli, C. tomentosa.*
Injury — Larvae burrow in smaller branches, killing them and producing gall-like swellings which weaken the branches so that they break in winds.
Distribution — Eastern North America.
Reference — Felt, E. P., and Joutel, L. H. New York State Mus. Bul. 74:62. 1904.

femorata Fabr., *Chrysobothris* (Flat-headed apple-tree borer) ..... Fam. *Buprestidae*
Hosts — Many trees, including Crataegus, but especially Quercus, Malus, Prunus.

Injury — Larvae burrow in sapwood of weakened trees.
Distribution — North America.
Reference — Brooks, F. E. U. S. Agr. Dept. Farmers' bul. 1065:5. 1919.

flavicornis Boh. Schn., *Anthonomus*.....Fam. *Curculionidae*
Hosts — Crataegus, Solanum, dogwood, and other species.
Distribution — North America.
Reference — Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 298. 1916.

flavicornis Clairv., *Ramphus*.....Fam. *Curculionidae*
Synonym — *Ramphus oxyacanthae* Marsh.
Hosts — Malus, *Crataegus oxyacantha*, Betula, Salix, Prunus, Populus.
Injury — Larvae mine in leaves.
Distribution — Europe.
References — Heyden, C. von. Berlin. ent. Zeit. 6:63. 1862.
Bargagli, P. Rincofori Europei, p. 251. 1883.

foliacea Lec., *Haltica* (Apple flea beetle).....Fam. *Chrysomelidae*
Hosts — Malus, Crataegus.
Injury — Beetles and larvae eat many small holes in foliage.
Distribution — North America.
Reference — Murtfeldt, M. E. Insect life 1:74. 1888.

giganteus Krinick., *Rhynchites*.....Fam. *Curculionidae*
Host — *Crataegus oxyacantha*.
Distribution — Europe, Asia.
References — Desbrochers, L. Monographie des Rhinomaceridae, p. 345. 1869.
Bargagli, P. Rincofori Europei, p. 180, 188. 1883.

helxines Linn., *Crepidodera*.....Fam. *Chrysomelidae*
Hosts — Crataegus, Salix, Malus, Pyrus, Ulmus, Populus.
Injury — Beetles eat many small holes in leaves.
Distribution — Europe, North America.
References — Blatchley, W. S. Coleoptera of Indiana, p. 1214. 1910.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 205. 1914.

icosandriae Scop., *Rhynchites*.....Fam. *Curculionidae*
Synonym — *Rhynchites conicus* Ill.
Hosts — *Crataegus oxyacantha*, Malus, Pyrus, Prunus, Sorbus.
Injury — Beetles cut off tender twigs. Serious pest in nurseries.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154, 207. 1872.
Bargagli, P. Rincofori Europei, p. 188. 1883.

impressifrons Gyll., *Polydrusus*.....Fam. *Curculionidae*
Hosts — Salix, Populus, Crataegus, Quercus, Malus, Pyrus, Corylus, and other species.
Injury — Beetles eat buds, leaves, and tender twigs in May and June.
Distribution — Europe, New York (imported about 1906).
References — Parrott, P. J., and Glasgow, H. New York (Geneva) Agr. Exp. Sta. Tech. bul. 56:7. 1916.
Pierce, W. D. Journ. econ. ent. 9:424. 1916.

maculicornis Germ., *Phyllobius* (Green leaf weevil).....Fam. *Curculionidae*
Hosts — Malus, Pyrus, Prunus, Quercus, Crataegus, Acer.
Injury — Beetle eats into opening buds, and later eats holes in leaves.
Distribution — Europe, Asia.
Reference — Theobald, F. V. Insect pests of fruits, p. 119. 1909.

marginalis Ill., *Systena*.....Fam. *Chrysomelidae*
(See page 1067.)

metasternalis Cr., *Tymnes*.....Fam. *Chrysomelidae*
Host — Crataegus.
Distribution — North America.
Reference — Smith, J. B. Insects of New Jersey, p. 344. 1909.

mixtus Lec., *Anthonomopsis*.....Fam. *Curculionidae*
Hosts — Crataegus, Prunus.
Distribution — North America.
Reference — Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 286. 1916.

multipunctata Say, *Calligrapha*.....Fam. *Chrysomelidae*
Host — Crataegus.
Distribution — North America.
Reference — Blatchley, W. S. Coleoptera of Indiana, p. 1158. 1910.

naso Lec., *Conotrachelus*.....Fam. *Curculionidae*
Hosts — Crataegus, *Quercus virginiana.*
Injury — Larva feeds in fruit.
Distribution — North America.
References — Hamilton, J. Can. ent. **21**:34. 1889.
Pierce, W. D. Nebraska State Bd. Agr. Ann. rept. **1906–07**:275. 1907.

nebulosus Lec., *Anthonomus* (Hawthorn blossom weevil).....Fam. *Curculionidae*
(See page 1068.)

nenuphar Hbst., *Conotrachelus* (Plum curculio).....Fam. *Curculionidae*
Hosts — Prunus, Pyrus, Malus, Cydonia, Crataegus.
Injury — Larvae feed in fruit, and beetles deform fruits by their feeding punctures.
Distribution — North America east of Rocky Mountains.
Reference — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 243. 1914.

nitidipennis Boh., *Magdalis*.....Fam. *Curculionidae*
Hosts — Crataegus, Populus, Salix.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Käfer, p. 759. 1858.
Bargagli, P. Rincofori Europei, p. 196. 1883.

oblongus Linn., *Phyllobius*.....Fam. *Curculionidae*
Hosts — Malus, Crataegus, Populus, Corylus, and other species.
Injury — Beetles eat into opening buds, and later eat leaves.
Distribution — Europe, Asia.
Reference — Bargagli, P. Rincofori Europei, p. 79. 1883.
Theobald, F. V. Insect pests of fruits, p. 119. 1909.

olivaceus Gyll., *Rhynchites*.....Fam. *Curculionidae*
Synonym — *Rhynchites comatus* Dej.
Hosts — Crataegus, Corylus, Prunus.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154, 207. 1872.
Bargagli, P. Rincofori Europei, p. 190. 1883.

pauxillus Germ., *Rhynchites*.....Fam. *Curculionidae*
Hosts — *Crataegus oxyacantha*, Malus.
Injury — Beetles cut off twigs.
Distribution — Europe.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Theobald, F. V. Insect pests of fruits, p. 118. 1909.

politus Say, *Agrilus* ..... Fam. *Buprestidae*
Hosts — Crataegus, Salix, Quercus, Corylus.
Injury — Larva tunnels under bark, causing gall-like swellings on twigs of Crataegus and girdling twigs of oak with a spiral tunnel.
Distribution — North America.
References — Smith, J. B. Insects of New Jersey, p. 295. 1909.
Felt, E. P. New York State Mus. Bul. 200:135. 1918.

pomonae Fabr., *Apion* ..... Fam. *Curculionidae*
Hosts — Vicia, Crataegus.
Distribution — Europe.
References — Curtis, J. Farm insects, p. 487. 1860.
Bargagli, P. Rincofori Europei, p. 165. 1883.

pomorum Linn., *Anthonomus* (Apple blossom weevil) ..... Fam. *Curculionidae*
Hosts — Malus, Pyrus, Crataegus.
Injury — Larva feeds within closed fruit bud, destroying it. Often a very serious pest of apple in Europe. Whitehead records shaking 1530 adults from a single tree in two days.
Distribution — Europe, one specimen recorded from Ohio taken among *A. nebulosus*.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Dietz, Wm. G. Amer. Ent. Soc. Trans. 18:204. 1891.
Whitehead, C. Report on injurious insects in Great Britain, p. 44. 1892.
Henschel, G. A. O. Die schädlichen forst- und obstbaum Insekten, p. 571. 1895.
Collinge, W. E. Manual of injurious insects, p. 97. 1912.

posticatus Boh. Schn., *Conotrachelus* ..... Fam. *Curculionidae*
Hosts — Crataegus, Prunus, Carya.
Injury — Larva feeds in fruit.
Distribution — North America.
References — Hamilton, J. Can. ent. 21:34. 1889.
Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 477. 1916.

profundus Lec., *Anthonomus* ..... Fam. *Curculionidae*
Hosts — Crataegus, Quercus.
Injury — Larva feeds in fruit.
Distribution — North America.
Reference — Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 290. 1916.

pruni Ratz., *Eccoptogaster* ..... Fam. *Ipidae*
Hosts — Malus, Pyrus, Prunus, Crataegus, Ulmus.
Injury — Larva girdles weakened trees by mining in cambium layer.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154. 1872.
Wahl, C. von. Borkenkäfer an den Obstbäumen und ihre Bekämfung. Augustenberg Flugblatt, no. 3, p. 4. 1914.

pruni Linn., *Magdalis* ..... Fam. *Curculionidae*
Hosts — Prunus, Crataegus, Rosa, and other species.
Injury — Larva tunnels under bark of branches.
Distribution — Europe, Asia.

References — Bargagli, P. Rincofori Europei, p. 196. 1883.
Pierce, W. D. Manual of dangerous insects, p. 132. 1917.

pterygomalis Boh., *Polydrusus*.....Fam. *Curculionidae*
Hosts — *Crataegus oxyacantha*, Prunus, Salix, Betula, Corylus, Fagus.
Injury — Beetles feed on foliage.
Distribution — Europe, Asia.
Reference — Pierce, W. D. Journ. econ. ent. 9:431. 19 6.

pubescens Melsh., *Agriotes*.....Fam. *Elateridae*
(See page 1066.)

pubescens Fabr., *Rhynchites*.....Fam. *Curculionidae*
Synonym — *Rhynchites cyanicolor* Schr.
Hosts — Crataegus, Corylus, Alnus, Quercus.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Bargagli, P. Rincofori Europei, p. 191. 1883.

quadrigibbus Say, *Tachypterus* (Apple curculio).....Fam. *Curculionidae*
Hosts — Malus, Crataegus, Amelanchier, Pyrus.
Injury — Larva feeds in fruit, beetles puncture fruit and young twigs.
Distribution — Eastern North America.
References — Brooks, F. E. West Virginia Agr. Exp. Sta. Bul. 126. 1910.
Mitchell, J. B., and Pierce, W. D. Ent. Soc. Washington. Proc. 13:53. 1911.

quercata Fabr., *Anthaxia*.....Fam. *Buprestidae*
Hosts — Crataegus, *Pinus strobus*, Cercis, and other species.
Injury — Larva bores in dead or dying branches.
Distribution — North America.
Reference — Knull, Josef N. Ent. news 31:6. 1920.

rufus Ol., *Orchestes*.....Fam. *Curculionidae*
Hosts — Ulmus, Quercus, Salix, Crataegus, Prunus.
Distribution — Europe.
Reference — Bargagli, P. Rincofori Europei, p. 217. 1883.

rugulosus Ratz., *Eccoptogaster* (Fruit-tree bark beetle).....Fam. *Ipidae*
Hosts — Prunus, Cydonia, Malus, Crataegus, Sorbus, Amelanchier.
Injury — Larva and adult mine in cambium layer of weak trees, frequently killing them.
Distribution — Europe, Asia, North America.
References — Gossard, H. A. Ohio Agr. Exp. Sta. Circ. 140. 1913.
Wahl, C. von. Borkenkäfer an den Obstbäumen und ihre Bekämfung. Augustenberg Flugblatt, no. 3, p. 4. 1914.
Swaine, J. M. Can. Agr. Dept. Bul. 14:52. 1918.

scheppardi Kirby, *Choragus*.....Fam. *Anthribidae*
Synonym — *Alticopus galeazii* Vill.
Host — *Crataegus oxyacantha*.
Injury — Larva burrows in dying twigs.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Käfer, p. 674. 1858.
Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.

sericeus Schal., *Polydrusus*.....Fam. *Curculionidae*
Hosts — Pyrus, Prunus, Crataegus, Malus, Fagus, Salix, Quercus, Alnus, and other species.
Injury — Beetles feed on buds and foliage.

Distribution — Europe, Asia, recently imported into United States (Indiana).
References — Kaltenbach, J. H. Pflanzenfeinde, p. 179. 1872.
Bargagli, P. Rincofori Europei, p. 59. 1883.
Pierce, W. D. Journ. econ. ent. **9**:428. 1916.

sericeus Hbst., *Rhynchites*.....Fam. *Curculionidae*
Synonym — *Rhynchites ophthalmicus* Steph.
Hosts — Crataegus, Corylus, Quercus, Betula.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154, 207. 1872.
Bargagli, P. Rincofori Europei, p. 191. 1883.

sinuatus Oliv., *Agrilus* (Sinuate pear borer).....Fam. *Buprestidae*
Hosts — *Pyrus communis*, Crataegus, Sorbus.
Injury — Larva tunnels in sapwood, making a zigzag mine.
Distribution — Europe, North America.
References — Smith, J. B. New Jersey Agr. Exp. Sta. Ann. rept. **15**:550. 1894.
Scrauer, P. Handbuch der Pflanzenkrankheiten **3**:487. 1913.

subspinosus Fabr., *Macrodactylus* (Rose chafer).....Fam. *Scarabaeidae*
Hosts — Vitis, Malus, Pyrus, Rosa, Crataegus, and other species.
Injury — Beetles feed on foliage, flowers, and fruit, and are sometimes very injurious.
Distribution — North America.
References — Hartzell, F. Z. New York (Geneva) Agr. Exp. Sta. Bul. 331:534. 1910.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 397. 1914.

testacea Kirby, *Dichelonycha*.....Fam. *Scarabaeidae*
(See page 1067.)

tomentosus Fabr., *Byturus* (Raspberry beetle).....Fam. *Dermestidae*
Hosts — Rubus, Crataegus, Malus, Pyrus.
Injury — Beetles feed on flowers and foliage.
Distribution — Europe.
References — Sorauer, P. Handbuch der Pflanzenkrankheiten **3**:472. 1913.
Bot. journ. London **5**:73. 1917.

tubulatus Say, *Idiostethus*.....Fam. *Curculionidae*
Hosts — Orchids, Crataegus.
Distribution — North America.
References — Pierce, W. D. Nebraska State Bd. Agr. Ann. rept. **1906–07**:284. 1907.
Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 404. 1916.

villosula Melsh., *Xanthonia*.....Fam. *Chrysomelidae*
(See page 1067.)

vittaticollis Rand., *Agrilus*.....Fam. *Buprestidae*
Hosts — Crataegus, *Prunus virginiana*, Amelanchier.
Injury — Beetles feed on foliage.
Distribution — Eastern United States.
Reference — Blanchard, F. Amer. ent. **5**:32. 1889.

Melanotus sp.....Fam. *Elateridae*
(See page 1066.)

LEPIDOPTERA

abbotti Swains, *Sphecodina*.....Fam. *Sphingidae*
Hosts — Vitis, Ampelopsis, *Crataegus tomentosa*.
Injury — Larvae feed on foliage.

Distribution — Eastern North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Beutenmueller, William. Hawk moths of the vicinity of New York City, p. 12. 1903.

achatana Fabr., *Olethreutes*.....Fam. *Tortricidae*
Hosts — Crataegus, Malus.
Injury — Larvae roll leaves and eat them.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Theobald, F. V. Insect pests of fruits, p. 81. 1909.

advenella Zk., *Rhodophaea*.....Fam. *Pyralidae*
Hosts — Crataegus, Pyrus.
Injury — Larvae tie leaves and eat them.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:216. 1910.

aescularia Schiff., *Anisopteryx* (March moth).....Fam. *Geometridae*
Hosts — Crataegus, Malus, Prunus, Pyrus, Quercus, Tilia, Ulmus, Acer, and other species.
Injury — Larvae feed on foliage, sometimes defoliating trees.
Distribution — Europe.
Reference — Theobald, F. V. Insect pests of fruits, p. 61. 1909.

americana Harris, *Acronycta*.....Fam. *Noctuidae*
(See page 1073.)

americana Harris, *Epicnaptera*.....Fam. *Lasiocampidae*
(See page 1075.)

americana Fabr., *Malacosoma* (Apple tent caterpillar).....Fam. *Lasiocampidae*
Hosts — Prunus, Malus, Crataegus, Sorbus, Rosa, Amelanchier, Quercus, Salix, and other species.
Injury — Larvae defoliate branches, living within a silken tent.
Distribution — North America.
References — Felt. E. P. New York State Mus. Memoir 8^2:550. 1906.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 112. 1914.

anatipennella Hüb., *Coleophora*.....Fam. *Elachistidae*
Synonym — *Coleophora tiliella* Zell.
Hosts — Crataegus, Quercus, Tilia, Corylus, *Prunus spinosa*.
Injury — Larva eats patches of green tissue from leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, **2**:400. 1910.

anglicella Stt., *Ornix*.....Fam. *Gracilariidae*
Hosts — Crataegus, Fragaria.
Injury — Larva mines in leaf.
Distribution — Europe, Asia, one record in Massachusetts.
References — Stainton, H. T. Natural history of the Tineina, 8:292. 1864.
Kaltenbach, J. H. Pflanzenfeinde, p. 171. 1872.
Dietz, W. G. Amer. Ent. Soc. Trans. **33**:294. 1907.
Spuler, A. Schmetterlinge Europas, **2**:410. 1910.

angustiorana Haw., *Capua*.....Fam. *Tortricidae*
Hosts — Crataegus, Laurus, Smilax, Pyrus, and other species.

Injury — Larva ties leaves together and feeds on them.
Distribution — Southern Europe, northern Africa, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, **2**:246. 1910.

antiqua Linn., *Notolophus* (Vaporer moth) ..... Fam. *Lymantriidae*
Hosts — Malus, Prunus, Rosa, Crataegus, Ulmus, Tilia, and other species.
Injury — Larvae defoliate branches.
Distribution — Europe, Asia, North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Theobald, F. V. Insect pests of fruits, p. 38. 1909.

argyrospila Walk., *Archips* (Fruit-tree leaf roller) ..... Fam. *Tortricidae*
(See page 1077.)

arthemis Dru., *Basilarchia* ..... Fam. *Nymphalidae*
Hosts — Crataegus, Salix, Tilia, Populus.
Injury — Larvae eat leaves, except midrib, beginning at apex.
Distribution — Eastern United States.
References — French, G. H. Butterflies of the eastern United States, p. 208. 1886.
Edwards, H. U. S. Nat. Mus. Bul. 35:27. 1889.

astyanax Fabr., *Basilarchia* ..... Fam. *Nymphalidae*
Hosts — Salix, Prunus, Malus, Tilia, Crataegus, and other species.
Injury — Larva eats leaf on both sides of midrib, beginning at apex.
Distribution — Eastern and southern United States.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 535. 1890.
Holland, W. J. Butterfly book, p. 184. 1898.

aterrima Wck., *Nepticula* ..... Fam. *Nepticulidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Germany.
Reference — Spuler, A. Schmetterlinge Europas, **2**:480. 1910.

atricollis Stt., *Nepticula* ..... Fam. *Nepticulidae*
Hosts — *Malus malus, Prunus spinosa, Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, **2**:479. 1910.

aurantiaria Esp., *Hibernia* ..... Fam. *Geometridae*
Hosts — Betula, Populus, Rosa, Quercus, Crataegus, and other species.
Injury — Larva eats leaves.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209, 218. 1872.
Spuler, A. Schmetterlinge Europas, **2**:98. 1910.

bajaria Schiff., *Hibernia* ..... Fam. *Geometridae*
Hosts — Prunus, Pyrus, Crataegus, Ligustrum, Syringa.
Injury — Larva eats foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 166. 1872.
Spuler, A. Schmetterlinge Europas, **2**:98. 1910.

betulae Zell., *Lithocoll tis* ..... Fam. *Gracilariidae*
Hosts — Crataegus, Pyrus, Cydonia, Betula.
Injury — Larva mines in upper side of leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 198. 1872.
Spuler, A. Schmetterlinge Europas, **2**:419. 1910.

betularia Linn., *Amphidasis* (Pepper-and-salt moth) ..... Fam. *Geometridae*
Hosts — Malus, Prunus, Crataegus, Quercus, Ulmus, Populus, Betula.
Injury — Larvae defoliate trees in late summer.
Distribution — Europe, Asia, Japan.
Reference — Theobald, F. V. Insect pests of fruits, p. 64. 1909.

bidentata Clerck., *Gonodontis* (Scalloped hazel moth) ..... Fam. *Geometridae*
Hosts — Corylus, Betula, Prunus, Crataegus, Pyrus, Quercus, and other species.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia, Japan.
Reference — Collinge, W. E. Manual of injurious insects, p. 138. 1912.

biscutana Wck., *Epiblema* ..... Fam. *Tortricidae*
Hosts — Betula, *Crataegus oxyacantha*.
Injury — Larva ties together terminal clusters of leaves and feeds within.
Distribution — Norway, Finland.
Reference — Spuler, A. Schmetterlinge Europas, **2**:283. 1910.

blandula Hulst., *Catocala* ..... Fam. *Noctuidae*
Host — Crataegus.
Injury — Larvae feed on foliage.
Distribution — Eastern United States, Canada.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 533. 1890.
Smith, J. B. Insects of New Jersey, p. 476. 1909.

brumata Linn., *Cheimatobia* (Winter moth) ..... Fam. *Geometridae*
Hosts — Fruit and forest trees (except conifers) and shrubs.
Injury — Larvae defoliate trees and may attack flowers or fruit.
Distribution — Europe, Asia, Greenland.
References — Ormerod, E. A. Manual of injurious insects, p. 338, 360. 1890.
Theobald, F. V. Insect pests of fruits, p. 50. 1909.
Med. Phytopath. Dienst. Wageningen, no. 3. 1916.

calanus Hüb., *Strymon* (Banded hair-streak) ..... Fam. *Lycaenidae*
Synonym — *Thecla falacer* Godart.
Hosts — Crataegus, Quercus, Hicoria.
Injury — Larva eats holes in leaves.
Distribution — United States and Canada.
References — Scudder, S. Butterflies of New England, **2**:885. 1889.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

caryae Harris, *Halisidota* (Hickory tussock moth) ..... Fam. *Arctiidae*
Hosts — Hicoria, Juglans, Malus, Cydonia, Crataegus, and other species.
Injury — Larvae eat foliage.
Distribution — United States east of Rocky Mountains.
Reference — Soule, Caroline G. Psyche **6**:158. 1891.

catax Linn., *Eriogaster* ..... Fam. *Lasiocampidae*
Hosts — Crataegus, Quercus, Populus, Betula.
Injury — Larvae defoliate branches, which they cover with silken tents.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, **1**:117. 1908.

cecropia Linn., *Platysamia* ..... Fam. *Saturniidae*
Hosts — Crataegus, Malus, Pyrus, Prunus, Salix, Acer, Syringa, and other species.
Injury — Larva eats leaves.
Distribution — North America east of Rocky Mountains.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Dickerson, Mary C. Moths and butterflies, p. 157. 1901.

cerisolella Pey., *Lithocolletis*.....Fam. *Gracilariidae*
Hosts — Crataegus, *Sorbus torminalis*.
Injury — Larva mines in leaf on under side.
Distribution — Southern France.
Reference — Spuler, A. Schmetterlinge Europas, 2:415. 1910.

chionosema Zell., *Olethreutes*.....Fam. *Tortricidae*
(See page 1077.)

chrysorrhea Linn., *Euproctis* (Brown-tail moth).....Fam. *Lymantriidae*
Hosts — Crataegus and most other deciduous trees.
Injury — Larvae defoliate trees.
Distribution — Europe, Asia Minor, New England States.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:132. 1908.

clerkella Linn., *Lyonetia*.....Fam. *Lyonetiidae*
Hosts — Pyrus, Prunus, Crataegus, Sorbus, Betula.
Injury — Larva makes serpentine mine in leaf.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 2:422. 1910.

coeruleocephala Linn., *Diloba* (Figure-8 moth).....Fam. *Noctuidae*
Hosts — Malus, Prunus, Crataegus, and other species.
Injury — Larva eats foliage, sometimes defoliating hawthorn hedges.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Theobald, F. V. Insect pests of fruits, p. 35. 1909.

cognataria Guen., *Lycia*.....Fam. *Geometridae*
(See page 1076.)

cognatellus Hüb., *Yponomeuta* (Hedge ermine moth).....Fam. *Yponomeutidae*
Hosts — *Crataegus oxyacantha*, Euonymus.
Injury — Larva eats leaves, sometimes stripping hedges.
Distribution — Europe.
References — Spuler, A. Schmetterlinge Europas, 2:444. 1910.
Noel, P. Jardinage 4:363. 1914.

concinna A. and S., *Schizura* (Red-humped apple caterpillar).....Fam. *Notodontidae*
Hosts — Malus, Crataegus, Prunus, Pyrus, and other species.
Injury — Larvae defoliate branches, feeding in a colony.
Distribution — North America.
References — Saunders, William. Can. ent. 13:139. 1 81.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 125. 1914.

concomitella Bnks., *Lithocolletis*.....Fam. *Gracilariidae*
Synonym — *Lithocolletis pomifoliella* Zell.
Hosts — Malus, Crataegus.
Injury — Larva mines in leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 198. 1872.
Spuler, A. Schmetterlinge Europas, 2:415. 1910.

congelatella Clerck., *Exapate*.....Fam. *Tortricidae*
Hosts — Crataegus, Sorbus, Prunus, Pyrus, Rubus, Berberis, Ligustrum, and other species.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2:254. 1910.

contaminana Hüb., *Acalla* ..... Fam. *Tortricidae*
Hosts — Crataegus, Prunus, Pyrus, Malus, Quercus, and other species.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2:245. 1910.

corylifoliella Haw., *Lithocolletis* ..... Fam. *Gracilariidae*
Hosts — Crataegus, Pyrus, Malus, Sorbus.
Injury — Larva mines in leaf.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 2:417. 1910.

crataegana Hüb., *Cacoecia* ..... Fam. *Tortricidae*
Synonym — *Penthina robrana* Schiff.
Hosts — Crataegus, Quercus, Betula, Populus, Malus, Cotoneaster, and other species.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2:247. 1910.

crataegella Clem., *Lithocolletis* ..... Fam. *Gracilariidae*
Hosts — Crataegus, Pyrus, *Prunus serotina*.
Injury — Larva mines in leaf.
Distribution — North America.
References — Braun, A. F. Amer. Ent. Soc. Trans. 34:301. 1908.
Wilson, H. F. Oregon Agr. Exp. Sta. Bien. crop pest and hort. rept. 2:119. 1915.

crataegella Linn., *Scythropia* ..... Fam. *Yponomeutidae*
Hosts — *Crataegus oxyacantha*, *Prunus spinosa*, Pyrus.
Injury — Larva spins a tent over the branch and eats the leaves within it.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 169. 1872.
Spuler, A. Schmetterlinge Europas, 2:443. 1910.

crataegi Linn., *Aporia* (Fruit-tree pierid) ..... Fam. *Pieridae*
Hosts — Crataegus, Pyrus, Malus, Prunus, Sorbus, Salix, Quercus, and other species.
Injury — Larva eats foliage, often stripping trees.
Distribution — Europe.
References — Bechstein, J. M., and Scharfenberg, G. L. Naturgeschichte der schädlichen Forstinsekten, p. 303. 1805.
Sasscer, E. R. Journ. econ. ent. 11:126. 1918.

crataegi Zell., *Bucculatrix* ..... Fam. *Lyonetiidae*
Host — Crataegus.
Injury — Larva mines in leaf and later feeds externally on leaf.
Distribution — Europe.
Reference — Stainton, H. T. Natural history of the Tineina, 7:68. 1862.

crataegi Saund., *Catocala* ..... Fam. *Noctuidae*
Host — Crataegus.
Injury — Larva feeds on foliage.
Distribution — Eastern North America.
References — Saunders, William. Can. ent. 8:72. 1876.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 532. 1890.

crataegi Linn., *Trichiura*.....Fam. *Lasiocampidae*
Hosts — Prunus, Crataegus, Corylus, Betula, Salix, Alnus.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, **1**:114. 1908.

crataegifoliella Clem., *Nepticula*.....Fam. *Nepticulidae*
Host — *Crataegus uniflora.*
Injury — Larva mines in leaf.
Distribution — Eastern United States.
Reference — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 534. 1890.

crataegifoliella Clem., *Ornix*.....Fam. *Gracilariidae*
Host — *Crataegus tomentosa.*
Injury — Larva mines in leaf.
Distribution — Eastern United States.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 534. 1890.
Dietz, W. G. Amer. Ent. Soc. Trans. *33*:292. 1907.

cuculla Esp., *Lophopteryx*.....Fam. *Notodontidae*
Synonym — *Notodonta cucullina* Hüb.
Hosts — *Acer campestre*, Crataegus.
Injury — Larva feeds on foliage.
Distribution — Europe.
Reference — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.

cucullatella Linn., *Nola*.....Fam. *Nolidae*
Synonym — *Hercyna palliolalis* Hüb.
Hosts — Prunus, Malus, Crataegus.
Injury — Larva eats foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, *2*:122. 1910.

curvilineella Chamb., *Blastodacna* (Hawthorn fruit miner).....Fam. *Cosmopterygidae*
(See page 1080.)

dactylina Grote, *Acronycta*.....Fam. *Noctuidae*
(See page 1073.)

defoliaria Linn., *Hibernia* (Mottled umber moth).....Fam. *Geometridae*
Hosts — Malus, Prunus, Betula, Corylus, Quercus, Crataegus, Pyrus, and other species.
Injury — Larvae defoliate trees.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 163. 1872.
Theobald, F. V. Insect pests of fruits, p. 58. 1909.

dispar Linn., *Lymantria* (Gipsy moth).....Fam. *Lymantriidae*
Hosts — Species a very general feeder on trees. Crataegus a favored food plant.
Injury — Larvae defoliate trees.
Distribution — Europe, Asia, New England States.
References — Spuler, A. Schmetterlinge Europas, **1**:131. 1908.
Mosher, F. H. U. S. Agr. Dept. Bul. 250. 1915.

disstria Hüb., *Malacosoma* (Forest tent caterpillar).....Fam. *Lasiocampidae*
Hosts — Acer, Quercus, Crataegus, Malus, and other species.
Injury — Larvae defoliate branches, feeding in colonies.
Distribution — North America.

References — Insect life 3:478. 1890.
Insect life 4:75. 1891.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 119. 1914.

dubitata Linn., *Triphosa*.....Fam. *Geometridae*
Hosts — Crataegus, Prunus, Rhamnus.
Injury — Larva webs leaves together and feeds on them.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 166. 1872.
Spuler, A. Schmetterlinge Europas, 2:36. 1910.

ephemeraeformis Haw., *Thyridopteryx* (Common bagworm).....Fam. *Psychidae*
Hosts — Species a very general feeder on trees and shrubs, including Crataegus.
Injury — Larva defoliates trees.
Distribution — North America east of Rocky Mountains.
Reference — Beutenmueller, William. Ent. Amer. 3:157. 1887.

ephippella Fabr., *Argyresthia*.....Fam. *Yponomeutidae*
Synonym — *Argyresthia pruniella* Linn.
Hosts — Crataegus, Pyrus, Prunus, Sorbus, Corylus.
Injury — Larva eats leaf and blossom buds.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2:447. 1910.

euphorbiae Fabr., *Acronycta*.....Fam. *Noctuidae*
Hosts — Species a general feeder on trees, including Crataegus.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:139. 1908.

fabriciana Linn., *Simaethis*.....Fam. *Glyphipterygidae*
Synonyms — *Tinea oxyacanthella* Linn., *Crambus oxyacanthae* Fabr.
Hosts — Urtica, Parietaria, Symphytum, Crataegus.
Injury — Larva feeds in leaf roll.
Distribution — Europe.
References — Bechstein, J. M., and Scharfenberg, G. L. Naturgeschichte der schädlichen Forstinsekten, p. 805. 1805.
Spuler, A. Schmetterlinge Europas, 2:297. 1910.

fasciellus Hüb., *Holcophora*.....Fam. *Gelechiidae*
Hosts — Prunus, Crataegus.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2:354. 1910.

fletcherella Fern., *Coleophora* (Cigar case-bearer).....Fam. *Elachistidae*
Hosts — Malus, Crataegus, Pyrus, Cydonia.
Injury — Larva eats holes into leaf and makes a small blotch mine around each hole.
Distribution — North America.
References — Hammar, A. G. U. S. Ent. Bur. Bul. 80:33. 1909.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 47. 1914.

fulminea Scop., *Catocala*.....Fam. *Noctuidae*
Synonym — *Catocala paranympha* Linn.
Hosts — Crataegus, Prunus, Pyrus, Quercus.
Injury — Larva eats foliage.

Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:317. 1908.

geminatella Pack., *Ornix* (Unspotted tentiform leaf miner of apple) ..... Fam. *Gracilariidae*
Synonym — *Lithocolletis prunivorella* Chamb.
Hosts — Crataegus, Pyrus, Prunus.
Injury — Larva mines in leaf.
Distribution — Eastern United States.
Reference — Haseman, L. Journ. agr. res. **6**:289. 1916.

glaucatus Schiff., *Cilex* ..... Fam. *Drepanidae*
Hosts — Prunus, Crataegus.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia.
References Kaltenbach, J. H. Pflanzenfeinde, p. 208. 187 .
Spuler, A. Schmetterlinge Europas, **1**:107. 1908.

gothica Linn., *Taeniocampa* ..... Fam. *Noctuidae*
Hosts — Crataegus, Tilia, Quercus, and other species.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:239. 1908.

gratiosella Stt., *Nepticula* ..... Fam. *Nepticulidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, **2**:476. 1910.

grotiana T., *Dichelia* ..... Fam. *Tortricidae*
Hosts — Crataegus, Quercus, Ulmus, Rubus, and other species.
Injury — Larva ties leaves and feeds on them.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, **2**:246. 1910.

hellerella Dup., *Blastodacna* ..... Fam. *Cosmopterygidae*
Hosts — Crataegus, Malus, Pyrus.
Injury — Larva tunnels in fruit of Crataegus and in fruit spurs and buds of apple.
Distribution — Europe.
References — Theobald, F. V. Insect pests of fruits, p. 92. 1909.
Spuler, A. Schmetterlinge Europas, **2**:387. 1910.

hemerobiella Scop., *Coleophora* ..... Fam. *Elachistidae*
Hosts — Crataegus, Pyrus, Prunus.
Injury — Larva eats star-shaped area from under side of leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, **2**:400. 1910.

heparana Schiff., *Pandemis* ..... Fam. *Tortricidae*
Hosts — Crataegus, Prunus, Sorbus, Malus, Alnus, Betula, Fagus, and other species.
Injury — Larva rolls leaf and feeds within the roll.
Distribution — Europe, Japan.
Reference — Spuler, A. Schmetterlinge Europas, **2**:249. 1910.

holmiana Linn., *Acalla* ..... Fam. *Tortricidae*
Hosts — Crataegus, Rosa, Prunus, Malus, Pyrus, Quercus.

Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, **2**:244. 1910.

ignobilella Stt., *Nepticula* ..... Fam. *Nepticulidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
Spuler, A. Schmetterlinge Europas, **2**:477. 1910.

incerta Hufn., *Taeniocampa* ..... Fam. *Noctuidae*
Synonym — *Taeniocampa instabilis* Hüb.
Hosts — Crataegus, Salix, Prunus, Quercus, Malus, and other species.
Injury — Larva eats leaves, and sometimes eats holes in apple fruit.
Distribution — Europe, Asia, South America.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Theobald, F. V. Insect pests of fruits, p. 66. 1909.

indigenella Zell., *Mineola* (Leaf crumpler) ..... Fam. *Pyralidae*
Synonyms — *Acrobasis nebulella* Riley, *Phycita nebulo* Walsh.
Hosts — Malus, Crataegus, *Hicoria pecan*, and other species.
Injury — Larva feeds on leaves, living in a case composed of leaf particles and silk.
Distribution — North America.
Reference — Riley, C. V. Fourth Missouri report, p. 42. 1872.

integerrima G. and R., *Datana* (Black-walnut caterpillar) ..... Fam. *Notodontidae*
Hosts — Juglans, Hicoria, Malus, Crataegus, and other species.
Injury — Larvae defoliate branches, feeding in a colony.
Distribution — Eastern United States.
Reference — Packard, A. S. Nat. Acad. Sci. Memoir 1:120. 1895.

inusitatumella Chamb., *Ornix* ..... Fam. *Gracilariidae*
Host — Crataegus.
Injury — Larva mines in upper surface of leaf.
Distribution — Eastern United States.
References — Chambers, V. T. Can. ent. **5**:48. 1873.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

io Fabr., *Automeris* ..... Fam. *Saturniidae*
(See page 1073.)

janthinana Dup., *Grapholitha* ..... Fam. *Tortricidae*
Synonym — *Tortrix incisana* Schiff.
Host — Crataegus.
Injury — Larva tunnels in fruit, then in twigs.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, **2**:294. 1910.

lacustrata Guen., *Mesoleuca* ..... Fam. *Geometridae*
Hosts — Rubus, Betula, Crataegus, Salix.
Injury — Larva feeds on foliage.
Distribution — Northeastern North America, Europe.
References — Packard, A. S. A monograph of the geometrid moths of the United States, p. 158. 1876.
Smith, J. B. Insects of New Jersey, p. 497. 1909.

lanestris Linn., *Eriogaster* ..... Fam. *Lasiocampidae*
Hosts — Prunus, Crataegus, Betula, Tilia, Salix.

Injury — Larvae defoliate branches, feeding gregariously in a white tent of silk.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:117. 1908.

leucatella Clerck., *Recurvaria* ..... Fam. *Gelechiidae*
Hosts — Crataegus, Pyrus, Prunus, Sorbus.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, **2**:356. 1910.

leucophaearia Schiff., *Hibernia* ..... Fam. *Geometridae*
Hosts — Quercus, Crataegus, Prunus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia, Japan.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:98. 1910.

leucostigma A. and S., *Hemerocampa* (White-marked tussock caterpillar) .. Fam. *Lymantriidae*
(See page 1075.)

limbata Haw., *Nematocampa* ..... Fam. *Geometridae*
Synonym — *Nematocampa filamentaria* Guen.
Hosts — Crataegus, Fragaria.
Injury — Larva eats foliage.
Distribution — North America.
References — Packard, A. S. A monograph of the geometrid moths of the United States, p. 471. 1876.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

parops Bdv. and Lec., *Strymon* (Striped hair-streak) ..... Fam. *Lycaenidae*
Hosts — Malus, Crataegus, Prunus, Amelanchier, Salix, Quercus, and other species.
Injury — Larva eats entire leaf and sometimes bores into fruit.
Distribution — United States, Canada.
References — Scudder, S. Butterflies of New England, **2**:877. 1889.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

ludifica Linn., *Trichosea* ..... Fam. *Noctuidae*
Hosts — Sorbus, Crataegus, Malus.
Injury — Larva eats leaves.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, **1**:135. 1908.

lunaria Schiff., *Selenia* ..... Fam. *Geometridae*
Hosts — Malus, Prunus, Crataegus, and other species.
Injury — Larva eats leaves.
Distribution — Europe, Asia.
Reference — Kaltenbach, J. H. Pflanzenfeinde, p. 165. 1872.

lutarea Haw., *Swammerdamia* ..... Fam. *Yponomeutidae*
Synonym — *Swammerdamia oxyacanthella* Dup.
Hosts — Crataegus, Sorbus.
Injury — Larva eats parenchymous tissue of leaves, which it ties together.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210, 782. 1872.
Spuler, A. Schmetterlinge Europas, **2**:445. 1910.

luteicoma G. and R., *Acronycta*.....Fam. *Noctuidae*
(See page 1073.)

luteolata Linn., *Opisthograptis*.....Fam. *Geometridae*
Synonym — *Rumia crataegata* Linn.
Hosts — Crataegus, Prunus, Malus, Pyrus, Sorbus.
Injury — Larva eats foliage.
Distribution — Europe, Asia, northern Africa.
Reference — Kaltenbach, J. H. Pflanzenfeinde, p. 165. 1872.

magnarius Guen., *Ennomos*.....Fam. *Geometridae*
(See page 1076.)

malifoliella Clem., *Tischeria* (Apple trumpet leaf-miner).....Fam. *Gracilariidae*
Hosts — Malus, Crataegus.
Injury — Larva mines in upper side of leaf, widening the mine gradually as it grows.
Distribution — North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Quaintance, A. L. U. S. Ent. Bur. Bul. 68:23. 1908.

malimalifoliella Braun, *Lithocolletis* (Spotted tentiform leaf miner of apple).Fam. *Gracilariidae*
Hosts — Malus, Cydonia, *Crataegus mollis*.
Injury — Larva mines in under side of leaf.
Distribution — Eastern United States.
Reference — Braun, A. F. Amer. Ent. Soc. Trans. 34:300. 1908.

malivorella Riley, *Coleophora* (Pistol case-bearer).....Fam. *Elachistidae*
(See page 1079.)

manteo Doub., *Heterocampa*.....Fam. *Notodontidae*
(See page 1074.)

marginaria Borckh., *Hibernia*.....Fam. *Geometridae*
Hosts — Crataegus, Betula, Quercus, Tilia, Populus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Spuler, A. Schmetterlinge Europas, 2:99. 1910.
Pierce, W. D. Manual of dangerous insects, p. 132. 1917.

melinus Hüb., *Strymon* (Common hair-streak).....Fam. *Lycaenidae*
Hosts — Hops, beans, Crataegus, and other species.
Injury — Larva eats leaves and sometimes bores into fruit.
Distribution — North America, Central America.
References — Scudder, S. Butterflies of New England, 2:850. 1889.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 535. 1890.
Crosby, C. R., and Leonard, M. D. Manual of vegetable garden insects, p. 84. 1918.

ministra Dru., *Datana* (Yellow-necked apple caterpillar).....Fam. *Notodontidae*
(See page 1075.)

myopiforme Bkh., *Trochilium*.....Fam. *Sesiidae*
Hosts — *Malus malus*, *Pyrus communis*, *Prunus domestica*, Crataegus.
Injury — Larva tunnels under bark of unhealthy trees.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2:310. 1910.

myops A. and S., *Paonias*.....Fam. *Sphingidae*
Hosts — Prunus, Crataegus, Salix, Corylus, and other species.
Injury — Larva eats leaves.

Distribution — Eastern United States.
Reference — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 525, 536. 1890.

naevana Hüb., *Rhopobota*.....Fam. *Tortricidae*
Hosts — Prunus, Crataegus, Malus, Rhamnus, Sorbus, Ilex, and other species.
Injury — Larva eats leaves of new shoots and ties them together.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, **2**:273. 1910.

nanella Hüb., *Recurvaria* (Lesser apple bud moth).....Fam. *Gelechiidae*
Synonym — *Recurvaria crataegella* Busck.
Hosts — Crataegus, Malus, Pyrus, Prunus.
Injury — Larvae destroy opening buds, and mine in leaves in late summer.
Distribution — Europe, North America.
References — Scott, E. W., and Paine, J. H. U. S. Agr. Dept. Bul. 113. 1914.
Sanders, G. E., and Dustan, A. G. Canada Agr. Dept., Ent. Branch. Bul. 16:33. 1919.

neustria Linn., *Malacosoma* (Lackey moth).....Fam. *Lasiocampidae*
Hosts — Malus, Pyrus, Prunus, Crataegus, Populus, Betula, Quercus, and other species.
Injury — Larva eats leaves, frequently defoliating fruit trees, and builds silken tent over colony.
Distribution — Europe, Asia.
References — Spuler, A. Schmetterlinge Europas, **1**:115. 1908.
Theobald, F. V. Insect pests of fruits, p. 30. 1909.

nitidella Fabr., *Argyresthia* (Cherry fruit moth).....Fam. *Yponomeutidae*
Hosts — Prunus, Crataegus.
Injury — Larva destroys young shoots of hawthorn, and bores into cherry fruit.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
Theobald, F. V. Insect pests of fruits, p. 192. 1909.
Spuler, A. Schmetterlinge Europas, **2**:447. 1910.

nitidella Hein., *Nepticula*.....Fam. *Nepticulidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Southwestern Germany.
Reference — Spuler, A. Schmetterlinge Europas, **2**:474. 1910.

nubeculana Clem., *Ancylis*.....Fam. *Tortricidae*
(See page 1077.)

nubilana Hüb., *Cnephasia*.....Fam. *Tortricidae*
Hosts — Crataegus, Pyrus, Prunus, Malus, Betula.
Injury — Larva feeds between leaves tied together with silk.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:253. 1910.

occidentalis G. and R., *Acronycta*.....Fam. *Noctuidae*
(See page 1074.)

ocellana Fabr., *Tmetocera* (Bud moth).....Fam. *Tortricidae*
Hosts — Crataegus, Sorbus, Malus, Pyrus, Cydonia, Prunus, Rubus, and other species.
Injury — Larva destroys buds in early spring, and later ties the leaves together and feeds on them.
Distribution — Europe, North America.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 192. 1872.
Slingerland, M. V. Cornell Univ. Agr. Exp. Sta. Bul. 107. 1896.
Theobald, F. V. Insect pests of fruits, p. 82. 1909.

oleagina Fabr., *Valeria*.....Fam. *Noctuidae*
Hosts — Crataegus, Prunus.
Injury — Larva feeds on foliage at night.
Distribution — Southern Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, **1**:185. 1908.

oreasella Clem., *Argyresthia*.....Fam. *Yponomeutidae*
(See page 1078.)

oxyacanthae Frey, *Lithocolletis*.....Fam. *Gracilariidae*
Host — *Crataegus oxyacantha*.
Injury — Larva mines in under side of leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
Spuler, A. Schmetterlinge Europas, **2**:415. 1910.

oxyacanthae Linn., *Miselia*.....Fam. *Noctuidae*
Host — *Crataegus oxyacantha*.
Injury — Larva eats foliage at night.
Distribution — Europe, Asia Minor.
References — Bechstein, J. M., and Scharfenberg, G. L. Naturgeschichte der schädlichen Forstinsekten, p. 504. 1805.
Spuler, A. Schmetterlinge Europas, **1**:204. 1908.

oxyacanthella Stt., *Nepticula*.....Fam. *Nepticulidae*
Hosts — *Crataegus oxyacantha*, *Malus malus*, Sorbus.
Injury — Larva mines in leaf on upper side.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 199. 1872.
Spuler, A. Schmetterlinge Europas, **2**:474. 1910.

padellus Linn., *Yponomeuta* (Hawthorn ermine moth).....Fam. *Yponomeutidae*
Synonym — *Hyponomeuta padella* Linn.
Hosts — Crataegus, Prunus, Vitis.
Injury — Larvae mine in leaves while young, then skeletonize leaves while living colonially in tents.
Distribution — Europe, North America (recently imported).
References — Theobald, F. V. Insect pests of fruits, p. 86. 1909.
Parrott, P. J. Journ. econ. ent. **11**:55. 1918.

pariana Clerck., *Simaethis*.....Fam. *Glyphipterygidae*
Hosts — Malus, Sorbus, Crataegus, Betula, Prunus.
Injury — Larva makes a slight web over the leaf, then skeletonizes it.
Distribution — Europe, Asia Minor, North America (recently imported).
References — Spuler, A. Schmetterlinge Europas, **2**:297. 1910.
Felt, E. P. New York State Mus. Bul. 202:33. 1917.

pedaria Fabr., *Phigalia*.....Fam. *Geometridae*
Hosts — Pyrus, Quercus, Betula, Prunus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 164. 1872.
Spuler, A. Schmetterlinge Europas, **2**:100. 1910.

podalirius Linn., *Papilio*.....Fam. *Papilionidae*
Hosts — Crataegus, Sorbus, Prunus, Amygdalus.
Injury — Larva eats foliage.
Distribution — Southern and central Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 1:2. 1908.

polygama Guen., *Catocala*.....Fam. *Noctuidae*
Host — Crataegus.
Injury — Larva feeds on foliage.
Distribution — Eastern North America.
References — Saunders, William. Can. ent. 8:72. 1876.
Edwards, H. U. S. Nat. Mus. Bul. 35:97. 1889.

polyphemus Cram., *Telea*.....Fam. *Saturniidae*
Hosts — Quercus, Ulmus, Juglans, Hicoria, Tilia, Betula, Rosa, Crataegus, and others.
Injury — Larva feeds on foliage.
Distribution — North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Dickerson, Mary C. Moths and butterflies, p. 169. 1901.

pometeria Peck, *Alsophila* (Fall cankerworm).....Fam. *Geometridae*
(See page 1076.)

pomifoliella Clem., *Bucculatrix* (Ribbed-cocoon-maker of apple).....Fam. *Lyonetiidae*
(See page 1079.)

pomonella Linn., *Cydia* (Codling moth).....Fam. *Tortricidae*
Hosts — Malus, Pyrus, Cydonia; occasionally Crataegus, Rosa, Prunus, *Juglans regia*.
Injury — Larva bores in fruit.
Distribution — Europe, Asia, North America, Africa, Australia.
References — Bruner, L. Nebraska State Hort. Soc. Rept. 1894:216. 1894.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 10. 1914.

populi Linn., *Poecilocampa*.....Fam. *Lasiocampidae*
Hosts — Populus, Tilia, Quercus, Ulmus, Betula, Salix, Crataegus, Malus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Theobald, F. V. Insect pests of fruits, p. 34. 1909.

porrinata Zell., *Nemoria*.....Fam. *Geometridae*
Hosts — Corylus, Crataegus, and other species.
Injury — Larva eats leaves.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 2:4. 1910.

praefica Grote, *Prodenia* (Yellow-striped army worm).....Fam. *Noctuidae*
Hosts — *Medicago sativa*, Vitis, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Pacific coast of the United States.
References — Essig, E. O. Injurious and beneficial insects of California, p. 401. 1915.
Crosby, C. R., and Leonard, M. D. Manual of vegetable garden insects, p. 295. 1918.

prunetorum Stt., *Nepticula*.....Fam. *Nepticulidae*
Hosts — Prunus, Crataegus.
Injury — Larva mines in leaf.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, **2**:476. 1910.

pruniana Hüb., *Argyroploce*.....Fam. *Tortricidae*
Hosts — Prunus, Sorbus, Rosa, Salix, Crataegus.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, **2**:265. 1910.

prunivora Walsh, *Laspeyresia* (Lesser apple worm).....Fam. *Tortricidae*
Hosts — Crataegus, Malus, Prunus.
Injury — Larva bores in fruit.
Distribution — North America east of Rocky Mountains.
Reference — Quaintance, A. L. U. S. Ent. Bur. Bul. 68:49. 1908.

psi Linn., *Acronycta* (Dagger moth).....Fam. *Noctuidae*
Hosts — Malus, Prunus, Crataegus, Salix, Rosa, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia, Japan.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Theobald, F. V. Insect pests of fruits, p. 41. 1909.

pudibunda Linn., *Dasychira* (Red-tail moth).....Fam. *Lymantriidae*
Hosts — Species a general feeder on fruit and forest trees. Crataegus a favored food plant.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Spuler, A. Schmetterlinge Europas, **1**:129. 1908.
Sorauer, P. Handbuch der Pflanzenkrankheiten, **3**:384. 1913.

purpuralis Linn., *Pyrausta*.....Fam. *Pyralidae*
Hosts — Mentha, Nepeta, Plantago, Crataegus.
Injury — Larva feeds on leaves spun together with silk.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:236. 1910.

pygmaeella Haw., *Nepticula*.....Fam. *Nepticulidae*
Hosts — *Crataegus oxyacantha*, *Malus malus*.
Injury — Larva mines in leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 199. 1872.
Spuler, A. Schmetterlinge Europas, **2**:473. 1910.

pyramidea Linn., *Amphipyra*.....Fam. *Noctuidae*
Hosts — Crataegus and many other trees.
Injury — Larva eats foliage.
Distribution — Europe, Asia, East Indies.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:238. 1908.

pyramidoides Guen., *Amphipyra*.....Fam. *Noctuidae*
Hosts — Crataegus and many other trees.
Injury — Larva eats foliage.
Distribution — North America.
Reference — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 171, 536. 1890.

pyri Harris, *Aegeria* (Pear borer) ..... Fam. *Sesiidae*
Synonym — *Sesia pyri* Boisd.
Hosts — Pyrus, Malus, Crataegus, Amelanchier, Prunus.
Injury — Larva burrows in bark and sapwood.
Distribution — Eastern United States.
Reference — Brooks, F. E. U. S. Agr. Dept. Bul. 887. 1920.

pyrina Linn., *Zeuzera* (Leopard moth) ..... Fam. *Cossidae*
Synonym — *Zeuzera aesculi* Linn.
Hosts — Pyrus, Malus, Prunus, Crataegus, Fraxinus, Populus, Betula, Ulmus, and other species.
Injury — Larva mines in solid healthy wood of branches.
Distribution — Europe, Asia, Japan, North America.
References — Lintner, A. J. Ninth report on injurious insects of New York, p. 426. 1893.
Theobald, F. V. Insect pests of fruits, p. 46. 1909.

quadrifasciana Fern., *Eulia* ..... Fam. *Tortricidae*
(See page 1078.)

quercifolia Linn., *Gastropacha* (Lappet moth) ..... Fam. *Lasiocampidae*
Hosts — Malus, Pyrus, Prunus, Crataegus, Quercus, and other species.
Injury — Larvae defoliate branches, especially of nursery trees, in spring.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:122. 1908.
Collinge, W. E. Manual of injurious insects, p. 137. 1912.

quercus Linn., *Lasiocampa* ..... Fam. *Lasiocampidae*
Hosts — Crataegus, Quercus, Betula, Salix, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:118. 1908.

quernaria A. and S., *Nacophora* ..... Fam. *Geometridae*
Hosts — Quercus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References — Packard, A. S. A monograph of the geometrid moths of the United States, p. 411. 1876.
Edwards, H. U. S. Nat. Mus. Bul. 35:106. 1889.

radcliffei Harv., *Acronycta* ..... Fam. *Noctuidae*
(See page 1074.)

regiella H. S., *Nepticula* ..... Fam. *Nepticulidae*
Host — *Crataegus oxyacantha*.
Injury — Larva mines in leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
Spuler, A. Schmetterlinge Europas, **2**:475. 1910.

rhediella Clerck., *Pamene* ..... Fam. *Tortricidae*
Hosts — Crataegus, Malus, Prunus, Cornus.
Injury — Larva feeds in fruit of Crataegus and also eats leaves.
Distribution — Europe, Asia Minor.
References — Theobald, F. V. Insect pests of fruits, p. 80. 1909.
Spuler, A. Schmetterlinge Europas, **2**:296. 1910.

ribeana Hüb., *Pandemis*.....Fam. *Tortricidae*
Hosts — Crataegus, Rosa, Prunus, Malus, Pyrus, Quercus, Sorbus, and other species.
Injury — Larva ties several leaves together and feeds within.
Distribution — Europe, Asia, Japan, East Indies.
Reference — Spuler, A. Schmetterlinge Europas, **2**:249. 1910.

rosaceana Harris, *Cacoecia* (Oblique-banded leaf roller).....Fam. *Tortricidae*
Hosts — Crataegus, Malus.
Injury — Larvae tie leaves together and feed on them.
Distribution — North America.
References — Essig, E. O. Injurious and beneficial insects of California, p. 441. 1915.
Sanders, G. E., and Dustan, A. G. Canada Agr. Dept., Ent. Branch. Bul. 16:30. 1919.

rosana Linn., *Cacoecia*.....Fam. *Tortricidae*
Synonym — *Tortrix laevigana* Schiff.
Hosts — Malus, Crataegus, Pyrus, Prunus, and other species.
Injury — Larvae tie leaves together and feed on them.
Distribution — Europe, Asia Minor, North America.
References — Theobald, F. V. Insect pests of fruits, p. 80. 1909.
Sorauer, P. Handbuch der Pflanzenkrankheiten, **3**:299. 1913.

scintillans Braun, *Nepticula*.....Fam. *Nepticulidae*
Host — *Crataegus mollis*.
Injury — Larva mines in leaf.
Distribution — Ohio.
Reference — Braun, A. F. Amer. Ent. Soc. Trans. **43**:167. 1917.

scitella Zell., *Cemiostoma* (Pear leaf blister moth).....Fam. *Lyonetiidae*
Hosts — Crataegus, Pyrus, Prunus, Sorbus.
Injury — Larva mines in leaf.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 197. 1872.
Theobald, F. V. Insect pests of fruits, p. 330. 1909.
Spuler, A. Schmetterlinge Europas, **2**:223. 1910.

scitula Harris, *Sesia*.....Fam. *Sesiidae*
(See page 1076.)

selenana Guen., *Ancylis*.....Fam. *Tortricidae*
Hosts — Pyrus, Malus, Crataegus.
Injury — Larva ties leaves together and feeds within.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, **2**:270. 1910.

signatana Dgl., *Steganoptycha*.....Fam. *Tortricidae*
Synonym — *Grapholitha kroesmanniana* Hein.
Hosts — Prunus, Crataegus.
Injury — Larva eats young terminal leaves after tying them with silk.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:276. 1910.

similis Fuessl., *Porthesia* (Gold-tail moth).....Fam. *Lymantriidae*
Synonym — *Liparis auriflua* Hüb.
Hosts — Crataegus and most other fruit and non-coniferous forest trees.
Injury — Larva eats foliage.
Distribution — Europe.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:133. 1908.

sphinx Hufn., *Brachionycha*.....Fam. *Noctuidae*
Synonym — *Asteroscopus cassinia* S. V.
Hosts — Quercus, Populus, Malus, Prunus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:203. 1908.

spiniana Dup., *Pamene*.....Fam. *Tortricidae*
Hosts — Crataegus, Prunus, Alnus.
Injury — Larva feeds in blossom, destroying it.
Distribution — Europe, northern Africa.
Reference — Spuler, A. Schmetterlinge Europas, 2:295. 1910.

splendoriferella Clem., *Coptodisca* (Resplendent shield-bearer).....Fam. *Elachistidae*
Hosts — Malus, Crataegus, *Prunus serotina*, Pyrus, Cydonia.
Injury — Larva mines in leaf and cuts out a small piece of the leaf for its case.
Distribution — Northeastern United States.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 75. 1914.

spurcella H. S., *Gelechia*.....Fam. *Gelechiidae*
Hosts — *Prunus spinosa*, *Crataegus oxyacantha*.
Injury — Larva rolls leaves.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2:361. 1910.

steinkelneriana Schiff., *Epigraphia*.....Fam. *Gelechiidae*
Hosts — Crataegus, Sorbus, *Prunus spinosa*, Fraxinus.
Injury — Larva ties leaves together and eats them.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2:332. 1910.

stimulea Clem., *Sibine* (Saddle-back caterpillar).....Fam. *Limacodidae*
Hosts — Species a general feeder on fruit and forest trees, including Crataegus.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References — Beutenmüller, William. Ent. Amer. 4:75. 1888.
Dyar, H. G., and Morton, E. L. New York Ent. Soc. Journ. 4:1. 1896.

strigata Müll., *Hemithea*.....Fam. *Geometridae*
Synonym — *Nemoria aestivaria* Hüb.
Hosts — Quercus, Crataegus, Corylus, Syringa, Malus, Prunus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia, Japan.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 163. 1872.
Spuler, A. Schmetterlinge Europas, 2:5. 1910.

strigosa Fabr., *Acronycta*.....Fam. *Noctuidae*
Hosts — Prunus, Crataegus, Rhamnus.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
Reference — Spuler, A. Schmetterlinge Europas, 1:137. 1908.

subsignarius Hüb., *Ennomos*.....Fam. *Geometridae*
(See page 1076.)

suffusana Z., *Notocelia*.....Fam. *Tortricidae*
Hosts — Crataegus, Prunus, Pyrus, Malus.
Injury — Larva ties together leaf cluster and feeds within, also eats leaf buds.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:279. 1910.

superans Guen., *Acronycta*.....Fam. *Noctuidae*
(See page 1074.)

tesselaris A. and S., *Halisidota*.....Fam. *Arctiidae*
(See page 1073.)

textor Harris, *Hyphantria* (Fall webworm).....Fam. *Arctiidae*
(See page 1073.)

thysbe Fabr., *Hemaris*.....Fam. *Sphingidae*
Hosts — Viburnum, Symphoricarpus, Crataegus.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References — Fernald, C. H. Sphingidae of New England, p. 16. 1886.
Beutenmueller, William. Hawk moths of the vicinity of New York City, p. 9. 1903.

tiliaria Harris, *Erranis* (Lime-tree spanworm).....Fam. *Geometridae*
(See page 1076.)

tineana Hüb., *Ancylis*.....Fam. *Tortricidae*
Hosts — Populus, Crataegus, Prunus, Malus.
Injury — Larva eats foliage after tying it with silk.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:270. 1910.

tirhaca Cr., *Pseudophia*.....Fam. *Noctuidae*
Synonym — *Ophiusa tirrhaea* Cr.
Hosts — Rhus, Pistacia, Crataegus.
Injury — Larva eats foliage.
Distribution — Southern Europe, Asia, Africa, Australia, and islands of southern Pacific.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:312. 1908.

titea Cram., *Phigalia*.....Fam. *Geometridae*
(See page 1076.)

trapezina Linn., *Calymnia*.....Fam. *Noctuidae*
Hosts — Quercus, Salix, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:244. 1908.

tridens Schiff., *Acronycta*.....Fam. *Noctuidae*
Hosts — Crataegus, Prunus, Malus, Rosa, Salix, Rhamnus, and other species.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:137. 1908.

turnus Linn., *Papilio* (Tiger swallowtail) ..... Fam. *Papilionidae*
Hosts — Crataegus, Malus, Cydonia, Prunus, Betula, Tilia, Quercus, Salix, and other species.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References — Saunders, William. Can. ent. 6:2. 1874.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

unicornis A. and S., *Schizura* ..... Fam. *Notodontidae*
Hosts — Malus, Prunus, Crataegus, Ulmus, Populus, Corylus, Quercus, and other species.
Injury — Larva eats foliage.
Distribution — North America.
Reference — Packard, A. S. Nat. Acad. Sci. Memoir 1:203. 1895.

variegana Hüb., *Olethreutes* ..... Fam. *Tortricidae*
Hosts — Malus, Pyrus, Crataegus, Prunus, and other species.
Injury — Larva ties leaf clusters together and eats leaves and buds.
Distribution — Europe, Asia.
References — Newstead, R. Gard. chron. **1901**:342. 1901.
Theobald, F. V. Insect pests of fruits, p. 82. 1909.

vernata Peck, *Paleacrita* (Spring cankerworm) ..... Fam. *Geometridae*
Hosts — Ulmus, Malus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — North America.
Reference — Wellhouse, W. H. Univ. Kans., Ent. Dept. Bul. 11:283. 1917.

vetusta Boisd., *Hemerocampa* (Western tussock moth) ..... Fam. *Lymantriidae*
Hosts — Malus, Prunus, Crataegus, Juglans, Quercus, and other species.
Injury — Larva eats leaves and sometimes young fruit.
Distribution — Pacific coast of the United States.
References — Branigan, E. J. State Comm. Hort. California. Mo. bul. 3:245. 1914.
Essig, E. O. Injurious and beneficial insects of California, p. 408. 1915.

viridana Walch., *Chariptera* ..... Fam. *Noctuidae*
Hosts — Prunus, Crataegus, Pyrus.
Injury — Larva eats foliage at night.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 1:204. 1908.

viridata Linn., *Nemoria* ..... Fam. *Geometridae*
Hosts — Calluna, Crataegus, Rubus, Quercus, Betula, Corylus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 235. 1872.
Spuler, A. Schmetterlinge Europas, **2**:4. 1910.

vulgata Haw., *Tephroclystia* ..... Fam. *Geometridae*
Hosts — Crataegus, Polygonum, Rubus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:75. 1910.

vulgella Hüb., *Gelechia* ..... Fam. *Gelechiidae*
Hosts — Crataegus, Prunus.

Injury — Larva ties together a cluster of leaves and feeds within.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, **2**:358. 1910.

DIPTERA

absobrina Felt, *Rhizomyia*..... Fam. *Cecidomyiidae*
Hosts — Crataegus, Populus, *Prunus virginiana.*
Injury — Larva found in leaf gall.
Distribution — North America.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

anthobia F. Loew, *Contarina*..... Fam. *Cecidomyiidae*
Host — *Crataegus oxyacantha.*
Injury — Solitary larva feeds in blossom bud, causing it to remain closed and swollen.
Distribution — Europe.
References — Ross, H. Die Pflanzengallen Mittel- und Nordeurcpas, p. 132. 1911.
Bagnall, R. S., and Harrison, J. W. H. Ent. Soc. London. Trans. **1917**:391. 1917.

bedeguar Walsh, *Cecidomyia* (Tufted thorn gall)..... Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larvae deform leaves with filamentous subglobular vein galls, 1 cm. long, generally found on the midveins.
Distribution — North America.
References — Walsh, B. D. Can. ent. **1**:79. 1869.
Felt, E. P. New York State Mus. Bul. 200:138. 1918.

cerasifolia Felt, *Mycodiplosis*..... Fam. *Cecidomyiidae*
Hosts — *Prunus virginiana*, Crataegus.
Injury — Larvae live in galls on hawthorn fruit caused by *Gymnosporangium clavipes*, and feed on the rust spores.
Distribution — North America.
References — Felt, E. P. New York State Mus. Bul. 200:152. 1918.
Wellhouse, W. H. Ent. news **30**:144. 1919.

circumdata Winn., *Perrisia*..... Fam. *Cecidomyiidae*
Host — *Crataegus oxyacantha.*
Injury — Larva lives in leaf gall.
Distribution — Germany.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 212. 1872.
Kieffer, J. J. Genera insectorum, fasc. 152, p. 75. 1913.

crataegi Winn., *Perrisia*..... Fam. *Cecidomyiidae*
Host — *Crataegus oxyacantha.*
Injury — Colonies of larvae cause rosettes of deformed sessile leaves, which make trees and hedges unsightly.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 212. 1872.
Connold, E. T. British vegetable galls, p. 190. 1902.

crataegifolia Felt, *Hormomyia* (Thorn cockscomb gall)..... Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larva deforms leaf with a green or red gall 1 cm. long, shaped like a cockscomb.
Distribution — United States.
References — Felt, E. P. Journ. econ. ent. **1**:20. 1908.
Felt, E. P. New York State Mus. Bul. 200:136. 1918.
(Figs. 116 and 117, page 1032.)

crataegifolia Felt, *Lestodiplosis* (Hawthorn fringed-cup gall) ..... Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larva causes a gall on leaf or twig.
Distribution — United States.
References — Felt, E. P. New York State Mus. Bul. 124:408. 1908.
Felt, E. P. New York State Mus. Bul. 200:138. 1918.
(Figs. 114 and 115, page 1081.)

excavata Felt, *Lasioptera* (Purple leaf blotch) ..... Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larvae deform leaves with green or reddish, blister-like mines, about 8 mm. in diameter.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

hirta Felt, *Rhizomyia* ..... Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Species probably inquiline in blister mine made by *Lasioptera excavata*.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

hudsonici Felt, *Winnertzia* ..... Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larva deforms leaf with stout, cup-shaped, fimbriate, unicellular gall.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

pomonella Walsh, *Rhagoletis* (Apple maggot) ..... Fam. *Trypetidae*
Hosts — Crataegus, Malus, Vaccinium, Symphoricarpos.
Injury — Larva tunnels in fruit.
Distribution — Eastern North America.
References — Walsh, B. D. First annual report on noxious insects of Illinois, p. 30. 1868.
O'Kane, W. C. New Hampshire Agr. Exp. Sta. Bul. 171. 1914.
Severin, H. H. P. State Comm. Hort. California. Mo. bul. 7:430. 1918.

venae Felt, *Lobopteromyia* (Thorn vein gall) ..... Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larva causes oval, smooth, fleshy gall, 5 to 8 mm. long, on leaf vein.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.
(Figs. 118 and 119, page 1083.)

venitalis Felt, *Dicrodiplosis* ..... Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larva found in same gall with *Lobopteromyia venae*.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

Cecidomyia sp. (a. 2727 Felt) ..... Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larvae cause subglobose, greenish, sometimes confluent, frequently pointed polythalamous vein galls, the under side reddish, diameter 3 mm.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

Cecidomyia sp. (a. 1840 Felt) (Thorn spindle gall) ..... Fam. *Cecidomyiidae*
Host — Crataegus.

Injury — Larva causes a spindle-shaped thickened gall on leaf vein, green or reddish, length 1 cm., diameter 2 mm.
Distribution — Eastern United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.
(Figs. 120 and 121, page 1084.)

HYMENOPTERA

betuleti Klg., *Trichiosoma* ..... Fam. *Tenthredinidae*
Synonyms — *Cimbex crataegi* Wd., *Trichiosoma tibialis* Steph.
Host — Crataegus.
Injury — Larva eats foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
André, Ed. Species des Hyménoptères d'Europe, 1:27. 1879.

cerasi Linn., *Caliroa* (Pear and cherry slug) ..... Fam. *Tenthredinidae*
Hosts — Prunus, Crataegus, Pyrus, and other species.
Injury — Larvae skeletonize leaves.
Distribution — Europe, North America, Australia.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 214. 1914.
MacGillivray, A. D. Hymenoptera of Connecticut, p. 79. 1916.

collaris MacG., *Profenusa* (Cherry and hawthorn sawfly leaf miner) .... Fam. *Tenthredinidae*
Hosts — Crataegus, *Prunus cerasus*.
Injury — Larva mines in leaf, causing brown blister which may cover from a quarter to the whole of the upper surface of the leaf.
Distribution — Massachusetts, New York.
Reference — Parrott, P. J., and Fulton, B. B. New York (Geneva) Agr. Exp. Sta. Bul. 411. 1915.

druparum Boh., *Syntomaspis* (Apple seed chalcid) ..... Fam. *Chalcididae*
Hosts — Malus, Pyrus, Sorbus, Crataegus.
Injury — Oviposition punctures cause dimples in fruit, and larvae destroy seeds.
Distribution — Europe, North America.
References — Schlechtendall, D. von. Ztschr. Naturwiss. Halle **61**:415. 1888.
Cushman, R. A. Journ. agr. res. 7:487. 1916.
Woodruffe-Peacock, E. A. Naturalist (London), no. 753, p. 329. 1919.

flaviventris Retz., *Lyda* ..... Fam. *Tenthredinidae*
Synonym — *Lyda clypeata* Klg.
Hosts — Crataegus, Pyrus.
Injury — Larvae defoliate branches, feeding in colonies.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 206. 1872.
André, Ed. Species des Hyménoptères d'Europe, 1:516. 1879.

humeralis Fourc., *Cimbex* ..... Fam. *Tenthredinidae*
Synonym — *Cimbex axillaris* Pz.
Hosts — Crataegus, *Prunus padus*.
Injury — Larva feeds on foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 212. 1872.
André, Ed. Species des Hyménoptères d'Europe, 1:24. 1879.

padi Linn., *Priophorus* ..... Fam. *Tenthredinidae*
Hosts — Crataegus, Pyrus, Prunus, Malus, Sorbus, and other species.
Injury — Larva skeletonizes leaves.
Distribution — Europe.
References — André, Ed. Species des Hyménoptères d'Europe, 1:84. 1879.
Collinge, W. E. Manual of injurious insects, p. 219. 1912.

punctum-album Linn., *Macrophya* ..... Fam. *Tenthredinidae*
Hosts — Fraxinus, Ligustrum, Crataegus.
Injury — Larva feeds on foliage.
Distribution — Europe.
Reference — André, Ed. Species des Hyménoptères d'Europe, 1:359. 1879.

Four species of unidentified sawflies (pages 1086 and 1087.)

INDEX OF GENERA AND SPECIES

(Synonyms are in italics)

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THE BIOLOGY OF THE CHRYSOPIDAE

ROGER C. SMITH

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CONTENTS

THE BIOLOGY OF THE CHRYSOPIDAE

THE BIOLOGY OF THE CHRYSOPIDAE[1]

ROGER C. SMITH

The insects included in the family Chrysopidae are of particular interest, first, because of their economic importance in destroying various small, soft-bodied noxious insects, spiders, and mites, and secondly, because of certain phases of their life history. Approximately sixty species of Chrysopidae have been designated in the United States. Several species in each locality can well be included in the list of common insects. They comprise one of the most homogenous families in habits and morphology to be found among insects.

The work herein described is based on the study of some fifteen species and covers a period of more than four years. The greater part of the work was done at Ithaca, New York, and additional collections and studies were made at Dayton, Ohio, at Milwaukee, Wisconsin, at Charlottesville, Virginia, and at Manhattan, Kansas. Through the courtesy of Dr. Nathan Banks, the writer was permitted to study the chrysopid types of Hagen, Fitch, and Banks now in the Museum of Comparative Zoology at Cambridge, Massachusetts.

Acknowledgment is made to Professor James G. Needham, of Cornell University, under whose direction this work was done. Further acknowledgment is made to Professor William A. Riley and to Mrs. R. C. Smith.

HISTORY OF THE FAMILY

Réaumur (1737) gave the first general discussion of this family, along with a discussion of the Hemerobiidae. This included a brief account of the habits, and a description, of three kinds of larvae. Linnaeus (1758) grouped the Chrysopidae with the Hemerobiidae under the name of the latter in his tenth edition of the *Systema Naturae.* The systematic position of the family remained unchanged until 1815, when Leach designated the family Chrysopidae, with the one genus Chrysopa, the name being derived according to Schneider (1851) from *Hemerobius chrysopis.*

Schneider's excellent monograph marked the real beginning of the modern classification of the family. From that time to the present, many species have been described by Brauer, Hagen, McLachlan, Petersen, and Navas.

In the United States, among the early writers was Fitch (1855), who gave a very excellent account of the Chrysopidae. He discussed the life history and biology of the species in New York State, and described all the species he could find. Hagen (1861) listed and described thirty-

[1]Also presented to the Faculty of the Graduate School of Cornell University, June, 1917, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

eight species, all under the genus Chrysopa except *Meleoma signoretti*. Banks (1903 and 1907) gives the present classification of the family, with the exception of some new species added since. He has contributed nearly all the descriptions of American species since Hagen's time.

METHOD OF STUDY

In these studies, chrysopid adults were confined in vials and lamp-chimney cages over growing plants, for oviposition. The vials (Plate LXXXV, 1) were plugged with cotton, and the chimneys were covered with several thicknesses of cheesecloth held in place by a rubber band. All adults and larvae were fed daily with the food on which they appeared to thrive best, which was in general the smaller aphids. The cabbage aphis, *Aphis brassicae*, was preferred for both larval and adult food. A constant supply of these insects was kept available on young cabbage plants throughout the fall, winter, and spring of each year. During the summer almost any species of aphid close at hand was used. A few drops of water in the vials was apparently relished by both larvae and adults. It was found advisable to occasionally moisten the cotton plugs of vials containing cocoons, in order to prevent the death of the pupae by desiccation.

All descriptions, photographs, and drawings of larvae were made by the writer from live material. Most of the photographed larvae were magnified from five to seven times and were but slightly reduced in reproduction. All drawings were outlined with a camera lucida. The drawings of corresponding parts were, with a few apparent exceptions, drawn to the same scale, so that they may be compared with one another as to size. Special effort was made to bring out identification characters in the illustrations. The dorsal setae have in most cases been extended forward. When studying a larva, the direction of these setae will be seen to vary with the position of the larva in the microscopic field. In reality, those over the thorax extend vertically, while those over the abdomen extend slightly caudad (Plate LXXV, 1).

LIFE HISTORY OF THE CHRYSOPIDAE

Most of the published information concerning the biology of this family is contained in brief notes by many writers. The two papers of Lurie (1897 and 1898) in Russian are important contributions. The most noteworthy work done in America is that of Fitch (1855), and that of Wildermuth (1916) on *Chrysopa californica*. The following references give either life histories or valuable biological information concerning the Chrysopidae, those marked with an asterisk being American papers.

Alderson, 1911—*Chrysopa dorsalis.*
Brauer, 1867—*C. pallida.*
*Fitch, 1855—*C. novaeboracensis* and others.
Froggatt, 1904—*C. ramburi.*
*Garman and Jewett, 1914—*C. oculata.*
*Howard, 1901—*C. oculata.*
LaCroix, 1921—*C. perla.*
*Lelong, 1890—*C. californica.*
Lurie, 1898—*C. septempunctata.*
*McGregor and McDonough, 1917—*C. rufilabris.*
*Marlatt, 1895—*C. oculata.*
Perkins, 1905—*C. microphya.*
Réaumur, 1737—General.
*Shimer, 1865—*C. illinoiensis.*
Van der Weele, 1909—*C. jacobsoni.*
*Weed, 1897—*C. oculata.*
*Wildermuth, 1916—*C. californica.*
Zehntner, 1900—*Chrysopa* sp.

The species studied biologically during their whole life history, or in part, for this account are as follows: *Chrysopa oculata* Say; *C. oculata* (Say) var. *albicornis* (Fitch); *C. oculata* (Say) var. *chlorophana* (Burm.); *C. chi* Fitch; *C. chi* (Fitch) var. *upsilon* (Fitch); *C. nigricornis* Burm.; *C. rufilabris* Burm.; *C. interrupta* Schn.; *C. quadripunctata* Burm.; *C. plorabunda* Fitch; *C. harrisii* Fitch; *C. lineaticornis* Fitch; *C. lateralis* Guér.; *C. bimaculata* McClend.; *C. cockerelli* Banks; *Meleoma signoretti* Fitch; *Allochrysa virginica* Fitch. The keys given by Banks (1903) will be found adequate for separating these genera and species.

Two species, *Chrysopa oculata* with its varieties, and *C. nigricornis,* have served almost equally as a basis for this account. These two were chosen because they are of wide distribution and because they represent two different habitats, the former being a garden and field species and the latter a tree species.

THE EGG

The eggs of the chrysopid species seen can be readily recognized and distinguished from the eggs of other insects by the fact that they are attached normally to a hyaline, hardened gelatinous stalk from four to eight millimeters long. The egg proper is elongate-elliptical in shape and green to yellowish green in color.

There is a difference in the size of the eggs of different species, as well as in the length of the stalk. There appears to be a slight variation also

in the color at deposition in some of the species, but the arrangement and the situation in which they are found have thus far been most useful in identification.

The color of the egg very closely simulates the green color of leaves. At first the eggs are of the same shade as is shown by the under side of most leaves of plants. As the embryo develops, the egg becomes gray with darker areas, but this change of color does not make it any more conspicuous.

The anterior pole of the egg is somewhat flattened. In the middle of this flattened area is the prominent, raised, button-like micropyle. The micropyle is circular and its center is depressed. The broad border is divided into from thirty to forty minute triangular ridges, with their outer borders rounded. The micropyle in *Chrysopa nigricornis* and that in *C. oculata* show exactly the same characteristics. It is white at all stages, but in freshly laid eggs it may have a slight greenish tinge.

The stalk of the egg

The egg stalk is composed of a hyaline gelatinous substance, which hardens somewhat after exposure to the air for a few seconds. In midsummer the stalks fail to harden to the same degree, due probably to the higher temperature. Then the stalk material may be drawn out like glue into a fine, clear thread. At all seasons the stalk hardens sufficiently to furnish a fairly rigid support for the egg and to withstand a strong wind. It is usually attached at the extreme posterior end of the egg, but in exceptional cases it may be attached to the side of the egg.

Usually there is one egg to a stalk, but confined females occasionally deposit an egg attached to the stalk or on the egg proper of a previously deposited normal egg. In one instance noted, two stalks were attached to the stalk of a previously deposited egg; in another instance, an unstalked egg was found adhering to a stalked egg.

The length of the stalk appears normally to vary directly as the length of the abdomen of the female. *Chrysopa nigricornis* was the largest species studied, and *C. plorabunda* the smallest. The stalks of the eggs of the former were the longest (from 7.57 to 8.6 millimeters), and those of the latter were the shortest (from 2.46 to 3.82 millimeters). Females in confinement, however, often deposit eggs on stalks half, or less than half, the normal length. Stalkless eggs are not uncommon, but these are evident abnormalities.

It is usually stated that the stalk is a protection against parasites and predatory enemies, particularly the larvae of their own kind. Eggs lying on a leaf are attacked as soon as the larvae become active, while the stalked eggs are generally the last discovered. Leaf crawlers, such

as Coccinellidae, Chrysomelidae, and various lepidopterous and hymenopterous larvae, are less likely to crush or to eat stalked eggs than unstalked ones. On the other hand, newly hatched and later first-instar larvae can ascend an egg stalk and exhaust the contents of the egg or the embryo. Generally speaking, newly hatched larvae first seek aphids or other food on the leaf surface, and climb the stalks after failing to find food there. Ants can climb up the stalks or bend them over and devour the eggs. They were very troublesome in outdoor rearing cages. Several species of hymenopterous parasites have been bred from chrysopid eggs. It is thus seen that the stalk offers only partial protection.

Location

Eggs may be deposited in a great variety of situations, depending on the species. The usual place is on plants provided with food for the larvae, not because the adult has the intuition to deposit them there, but because she goes to these plants to feed, and, being there, she deposits her eggs. Some of the less common species did not oviposit in confinement, but most species oviposited freely.

Some eggs have been observed in very unusual places. The shades and supports of the electric lights visited during the summer were often observed to have eggs deposited on them. Hundreds were deposited constantly in these unfavorable places. These eggs developed just as did eggs more favorably located, the empty shells always being found. A student reported that a female Chrysopa flew in through his open bedroom window when the light was on in the evening, and the next morning he found eggs deposited on his coat, which was hanging over a chair. In another student's room, the writer observed two hatched Chrysopa eggs on the chandelier. Brick and stone walls near lights and near aphid-infested plants were frequently found to be places of oviposition. Since the larvae are very active, some of those hatching in such unfavorable places undoubtedly succeed in finding food, but many must perish.

Arrangement of the eggs

Eggs laid in the open generally do not have a definite arrangement. Occasionally a straight row of ten or fifteen almost equally distant may be found across a leaf or on a plant stem. Otherwise the eggs are deposited singly or in irregular groups at varying distances apart. *Chrysopa nigricornis* generally deposits its eggs in rather closely arranged, irregular groups on leaves of maples, spiraea, and other plants. Not infrequently they are in irregular tangled masses without any definte arrangement. Such groups can often be identified posi-

tively in the field as eggs of this species, but single eggs are not unusual.

Most of the eggs of *C. quadripunctata, C. rufilabris, C. chi,* and others of the more uncommon species, are laid singly. *C. oculata* and its varieties lay their eggs either singly or in irregular groups.

Eggs from fertilized females in rearings nearly always hatch, the hatching percentage approaching 100 if conditions are not decidedly unfavorable. In early spring and late fall rearings, the hatching percentage is lower. In one case in which 95 eggs were laid in the laboratory in February, 1916, by *C. oculata,* only 37 or 39 per cent hatched. This is an extremely low percentage, and was undoubtedly due to unfavorable temperature during the cold nights of February and March. However, examination of the unhatched eggs showed that the embryos of some were partly developed. No eggs from unfertilized females have hatched. They shrivel early, but retain their bluish green color.

In two experiments, eggs of *C. oculata* that were completely submerged up to nineteen hours, hatched, but eggs submerged in water for from twenty-four to forty-eight hours all failed to hatch. It is very probable that eggs can withstand considerable rainy weather and submergence for a short time as a result of floods, without injury.

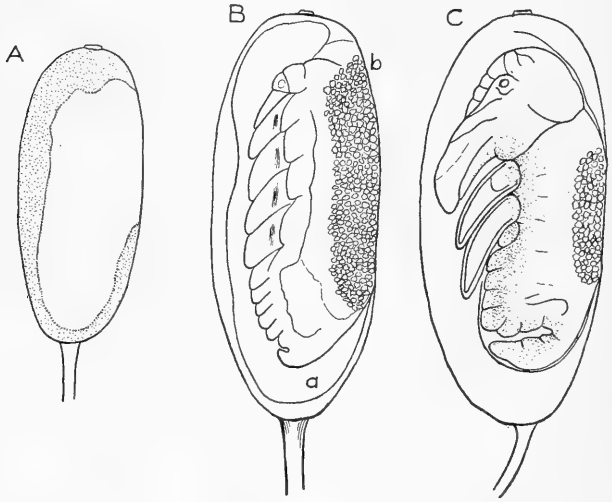


FIG. 154. EGGS AT VARIOUS STAGES

A, Lateral view of egg of Chrysopa oculata after thirty hours development, showing how the abdomen extends around on the dorsum in the early stages of development. B, Lateral view of egg of C. nigricornis after about ninety hours development, showing shortening of abdomen (a) at turning. C, Egg of C. nigricornis showing abdomen pushing forward toward the venter, thus completing the turning

Development of the embryo

The development of the embryo can be observed readily in Chrysopa eggs. The embryology has been the subject of short articles by several writers, among them Packard (1871 and

1872) and Tichomirowa (1890). The embryological observations made in the course of the present studies are not included in this account.

The chief point observed in the embryology which has not been described, it is believed, is the turning or partial turning of the embryo. The germ band develops on the venter of the egg, with the area destined to be the end of the abdomen extending around the posterior pole of the egg and part way up the side of the dorsum. At thirty hours the abdomen can be seen clearly in this position on the basal dorsal part of the egg. As development proceeds, the abdomen shortens and is drawn up in a fold at the posterior pole. As the dorsum of the embryo continues to envelop the yolk mass, the contracted abdomen pushes forward and comes to lie on the venter of the egg, reaching nearly to the tips of the jaws. The dorsum of the embryo has by that time enveloped the yolk mass and lies next to the chorion. This is the position of the embryo at hatching.

The large black ocellar areas appear very prominent in eggs ready to hatch, at the anterior end of the egg on each side of the midventral line. There is a lateral indenture of the chorion on each side extending nearly the length of the egg. There is a series of three or more somewhat triangular, very dark to black, bars at the sides. The egg burster can be seen as a narrow black line between the eyes in the midventral line.

There is considerable variation in the length of the period of development within the species. Temperature is undoubtedly the most important factor, as this variation is between different batches of eggs and is only slight in the same group. Eggs laid in the late fall or early spring were found to be the longest in development. The longest and the shortest records of embryonic development for a few species studied were: for *Chrysopa oculata,* from 5 to 12 days; for *C. nigricornis,* from 4 to 7 days; for *C. quadripunctata,* from 4 to 6 days.

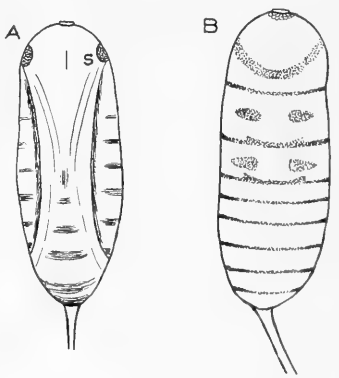


FIG. 155. EGGS OF CHRYSOPA OCULATA

A, Ventral view of egg ten minutes before hatching, showing the egg burster (s) in position. B, Dorsum of an egg ready to hatch

Hatching

One can readily ascertain when an egg will hatch by the distinctness with which the egg burster appears. Just before hatching, it is dark or black and one can scarcely tell whether it is through the chorion or just beneath it.

The embryo pushes the burster through the chorion to its entire length, and may by upward shifts widen the rent. Then its head is forced through the rent, causing the chorion to tear above. The head of the embryo bursts through the embryonic molt at this time or earlier, so that the molt, with the burster, is left behind. The molt is attached to the inside of the chorion in the midventral line. The mouth parts and the legs retard emergence so that the larva forms a loop over the egg. The mouth parts are slowly withdrawn from the molt, and then the larva emerges fully with the exception of the end of the abdomen. The larva then rests supported by the tip of the abdomen until the chitin hardens, and in a half hour from the beginning of hatching it is ready to descend from the shell. (Smith, 1922.)

The egg burster in Chrysopa oculata

The egg burster may be readily studied by picking out the embryonic molt from the lower part of the opening in the egg shell and mounting it in glycerin jelly or balsam. The burster is a thickening and specialization of the chitinous embryonic molt over the anterior mid-dorsal region of the head of the embryo. The burster proper is almost transparent and is 0.118 millimeter long and 0.029 millimeter wide at the lobe. In cross section it would appear V-shaped with the apex outward. Along the front border is a row of very small teeth which suggest a saw. The number of teeth varies from twenty to thirty and they are irregularly spaced. On the upper part is a prominent projection, referred to as a *lobe*. This lobe may or may not have a short, sharp tooth at its apex, but it bears teeth on the under side. The bursters of the species studied are all of this type.

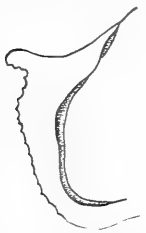


FIG. 156 EGG BURSTER OF CHRYSOPA NIGRICORNIS. LATERAL VIEW

THE LARVA

General characteristics

The larva at hatching is about 2 millimeters long, is sparsely beset with long setae, and is predominately gray in color. The average measurements of five newly hatched larvae of *Chrysopa oculata* were as follows:

Total length of larva	1.88 millimeters
Length of head	0.54 millimeter
Length of mandibles	0.34 millimeter
Width of head	0.33 millimeter
Width of body at metathorax	0.38 millimeter
Length of longest setae on body	0.47 millimeter

One can distinguish the first instar of all species in an easier and quicker way than by measurement. The lateral tubercules on prothorax and abdomen bear two setae each in this instar. The meso- and metathoracic tubercles bear three large setae each. But in no case are there from five to fifteen, as in the other instars. *C. oculata* and its varieties, and *C. chi* and its variety, have on the dorsum of the head a large black spot covering most of this area and broadening out to the bases of the antennae. This spot persists in the second instar, but in the third it breaks up into three spots. A few specimens show even in the first instar the future lines of separation, so that they may at times appear slightly disconnected. This large spot on the head, therefore, taken in connection with the size, will often indicate the instar at a glance. The head spots of the first-instar larvae of the other species studied are the same as in the second and third instars, and therefore the lateral setae furnish the more reliable index.

The color of the body changes gradually, so that at the end of the first instar the larva has, more or less distinctly, second-instar coloration. Larvae that have when mature a dark metathoracic region, begin to show this coloration about midway in the first instar. Abdominal coloration appears also at this time. But in all larvae the anterior part of the abdomen, regardless of future colors, appears smoky to black. This darkening is due to the food in the mid-intestine and appears with the first meal. In newly hatched larvae the green yolk can be seen in the mid-intestine at the posterior part of the thorax and the anterior part of the abdomen.

The legs, the jaws, and the antennae are nearly hyaline at hatching. Very soon the tips of the jaws become amber-colored, indicating chitinization. The legs and the antennae also darken slightly.

The lateral and dorsal setae serve both as a protection and as sense organs. When one of these setae is touched, the larva bends away from the object. If touched again the larva moves still farther away, or becomes frightened and runs away. The body of the larva can scarcely be touched without the larva's being apprised of the approach through these radiating setae. The dorsal setae serve to protect the dorsum, while the lateral ones protect the sides. The strong jaws are in front, and the abdomen can be retracted in part, so that the larva has a fair degree of security from its enemies.

Descent from the egg

The larva, after resting on the egg shell for from fifteen minutes to several hours, begins to walk around over the shell, at times reaching upward and outward in an effort to locate something near at hand by

which it can leave the egg. It holds fast by the tail except when bringing the abdomen forward; then it braces itself securely with its legs. It becomes more and more restless on the egg. Finally, after walking around over the egg, it discovers the egg stalk. If the stalk be perpendicular, the larva generally goes down head first, holding fast by the tail and grasping the stalk by the claws. Sometimes definite steps are indicated by the tail, but oftener this fails to hold and then it catches itself. The larva may come down backward, but this method appears to be less frequent. If the stalk be leaning or horizontal, the larva swings around on it and walks to the supporting surface upside down and head first. It grasps the stalk as a sloth grasps the limb of a tree. It does not use the tail in this case. Some writers suggest that the larva may drop from the egg. Lurie (1898), however, has stated correctly that dropping from the egg is not the normal manner of descent.

The larva is usually hungry by the time it comes down from the egg, and immediately it begins to search for food. If none is provided, it starves to death in about a day, or at most two days, after hatching. Small aphids, such as cabbage aphids, are best suited for feeding newly hatched larvae. Insects' eggs, such as those of aphids and of the corn-ear worm moth, have also been used in rearings.

If a leaf having on it a group of eggs ready to hatch is left in a vial, the cannibalistic habits of the larvae will be demonstrated. In the same batch of eggs, those first deposited or those developing most rapidly will hatch first. If the larvae are undisturbed and are not fed, they will attack the unhatched eggs and then one another. In one instance forty-one eggs were allowed to hatch. After a few days there was but one live larva, the others having been killed by it or by its companions.

Molting

All chrysopid larvae have been observed to molt three times, the last molt occurring within the cocoon. This does not include the embryonic molt, which occurs at hatching.

The first molt takes place from two to seven days after hatching. The second molt usually occurs at a somewhat shorter interval, from two to five days. The third instar may be very prolonged. Spinning usually takes place from four to ten days after the second molt. The final larval molt within the case occurs from five to fifteen days after spinning, or, in the case of wintering forms, from four to eight months after spinning.

First molt

In *Chrysopa oculata,* the appearance of the chitin at the time of the molting is shining and glassy. On closer study, the stout setae so characteristic of second-instar larvae can be seen regularly folded across the body beneath the old first-instar cuticula. The setae of the prothoracic tubercles are folded ventrad and caudad. They fold, therefore, around the body, and come together on the midventral line. Where it occurs, this prominent black line on the venter is one of the best indices of early molting. The setae of the other thoracic and the abdominal tubercles are folded across the dorsum. They are dark to black, and become fairly distinct just before molting. The old setae appear wholly black and somewhat shriveled. The ends of many are bent downward or broken. Most of them appear to be more or less withered. The coloration of the second instar can also be seen, but instead of appearing sharp and brilliant, the colors are dull and indistinct.

Just prior to molting, the larva takes no food. Some time before molting, it generally engorges with food; but just prior to the process, aphids may walk over the larva without being attacked. The larva also experiences some difficulty in walking at this time. It appears that the pulvilli do not adhere well to the substratum; their hold slips, and apparently the anal secretion is too copious and this also retards them. In all species the head capsule is somewhat distorted, especially posteriorly.

As a typical case the molting of a first-instar larva of *C. oculata,* as observed under the highest-power binocular, is here described. This larva was observed to be ready to molt, and with a camel's-hair brush it was removed to a slide. Soon there was noted a drop of a gelatinous anal secretion, which held the tail to the slide. The larva began to twist and pull. The legs appeared to be practically useless. The segments of the tail began to contract as units, in regular order, beginning with the last and going forward about every seven seconds. This continued for four and one-half minutes. The end of the abdomen was then seen to free itself of the molt, which was shown by a shift forward. The contractions continued, and in a half minute the cuticula was free over the thorax and the abdomen also. It must next be forced open. The body was pulled forward by a series of wavelike contractions, comparable to those seen in the hatching embryo and the molting pupa. With each forward pull there was left a little more clear space in the tail region, and the thorax became more distended. The old cuticula during this process remained securely cemented to the slide by the end of the abdomen, this constituting the fixed point on which the larva pulled. After three or four rapidly repeated shifts, a split began on the mid-dorsal

line at the posterior part of the prothorax. This occurred six minutes after the abdomen was cemented to the slide. The split lengthened rapidly, both anteriorly and posteriorly. At the same time the thorax began to arch, the head was bent ventrad, and the abdomen was pulled forward. In two minutes more the mouth parts were very carefully and slowly withdrawn. The head was lifted slowly with the arching of the thorax, and during this process the legs were being withdrawn also. The tracheal chitinous intima was drawn out through the spiracles as hollow threads. The jaws and the antennae freed, the legs were pulled entirely out, the metathoracic legs being the last to appear. By this time the abdomen was practically out of the skin. The whole process to this stage required eight and a half minutes. As the old skin moved backward, the setae, folded across or around the body, thus freed, sprang into their normal positions.

The newly molted larva is very helpless, similar to its condition at hatching. The legs cannot be used. The head is bent ventrad and caudad. The larva holds fast to the molted skin by means of the anal proleg, which constitutes its only support while the new chitin is hardening. The legs are pulled up and then extended occasionally, and the head is slowly lifted to a horizontal position. The larva under observation rested on its legs and the head was in the normal position in twelve minutes from the beginning of the molt.

The old larval skin remained attached to the slide, the end of the tail being flattened and glued fast. There was a rent in the cast skin from the mesothorax to the head; in fact, only the venter of the thorax remained intact. The legs were pulled up and were wholly under the venter, except the last pair, which protruded slightly. The black patch on the head was retained. It is generally possible to name the species of the larva and the instar from the old larval skin. However, the color pattern is not well retained. In rearings, the molted skins were usually found in the vials adhering to the glass or to the cotton plugs.

The coloration of the body is that which is characteristic of the instar. The color pattern is distinct, of the greatest intensity during the instar. The grays at this time appear white to semi-translucent and often yellowish. The color pattern on the head is represented at molting, as at hatching, by an indistinct brownish patch. After an hour the outline of the black patch is distinct, but from two to four hours must pass before the normal head and body coloration is complete. The mouth parts, palpi, antennae, and legs are from wholly hyaline to translucent. The tips of the jaws become yellowish brown in an hour. The darkening of the leg segments appears slowly also.

Food offered to the larva up to forty-five minutes after emergence was rejected, but at the end of one and one-half hours the larva attacked a large aphid of its own accord and exhausted the fluids.

Later molts

About four days after the first molt, another molt occurs. The second molt is effected exactly like the first.

The final molt cannot be observed through the cocoon, but one can readily tell when the larva has pupated by the dark disk at the bottom of the cocoon. If a cocoon showing this disk be opened, it will be seen that the disk is the last larval skin which is pushed off the abdomen and rests at the bottom of the case. This molt may be observed if the larva fails to spin a cocoon, which can be brought about by disturbing it while it is spinning. It generally refuses to spin further if disturbed, and coils up in the bottom of the vial and pupates (Plate LXXXVII, 16). The old larval skin splits over the thorax, and by the raising and lowering of the head the skin is slowly moved back (Plate LXXXVII, 5). Further movements up and down on the thorax and the abdomen cause the skin to slip over the abdomen, and it finally rests near the end of the abdomen at the bottom of the cocoon.

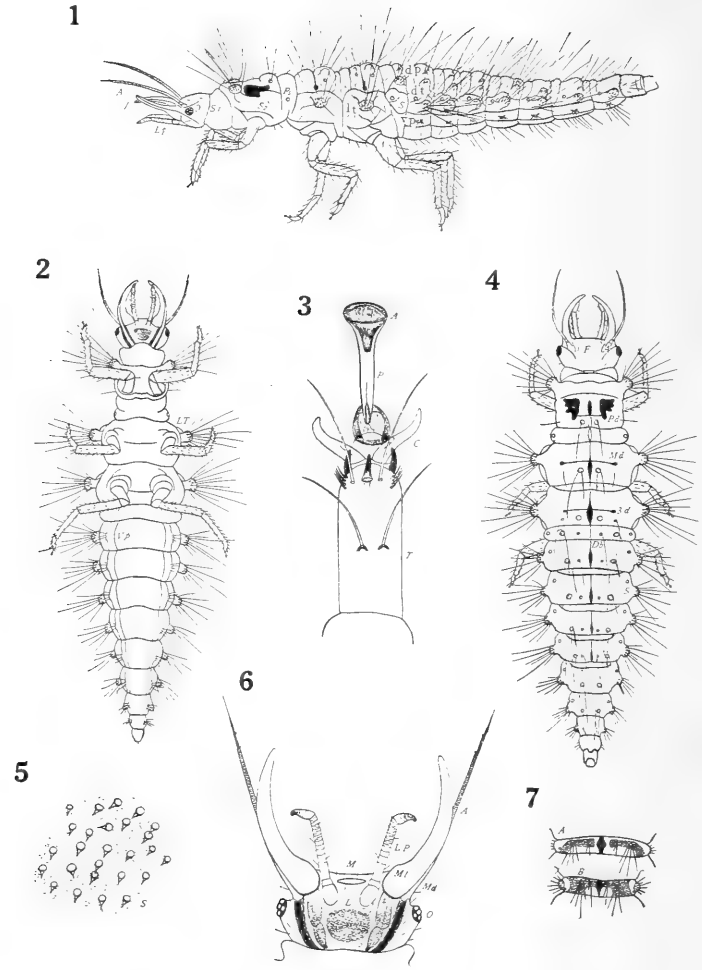
The trash carriers present complications in the molting process in that they carry packets of debris on their backs. In the few cases observed, the packet was cast off at the molting time and was reformed of fresh materials. If there were no fresh materials provided, the old packet was reappropriated. Lefroy (Lefroy and Howlett, 1909) described a similar form in India which carried such a packet, and stated that the packet was shed with each molt and was reformed from new materials.

Morphology

A number of very interesting features are illustrated by the morphology of the larva. The original somewhat detailed account must be omitted for the sake of brevity, and only a few features are here included.

Perhaps the most striking specialization in the family is the prolongation of the maxillae and the mandibles to form sucking tubes. These are held together by a flange which fits into a groove, and the small canal between them serves to convey their liquid food to the pharynx. The true mouth is mechanically closed, but may be opened by probing with a dissecting needle. It is somewhat reduced in size.

In the thorax and the abdomen, each segment is made up of two parts, or subsegments, which are in most cases quite apparent. The anterior subsegment is very much smaller than the posterior one. The



CHRYSOPA OCULATA AND C. NIGRICORNIS

1, Side view of a third-instar larva of Chrysopa oculata (A, antennae; J, jaws; Lp, labial palpi; O, ocellar field; S1, first subsegment, S2, second subsegment, of prothorax; lt, lateral tubercle; Ps, mesothoracic spiracle; dp, dorsal papilla; dt, dorsal tubercle; vp, ventral papilla)

2, Ventral view of same larva (LT, lateral tubercle; Vp, ventral papilla)

3, Tarsus and pulvillus of third-instar larva of C. oculata (A, arolium; P, plantula; C, claw; T, tarsus)

4, Dorsal view of larva shown in 1 and 2 (Pd, prothoracic depression, Md, mesothoracic depression, 3d, metathoracic depression, all probably apodeme invaginations; Db, dorsal blood vessel; A, antennal sclerite; F, front; S, spiracle)

5, External appearance of cuticula of a mature larva, under high magnification (S, spinules)

6, Ventral view of head of third-instar larva of C. oculata (A, antenna; Md, mandible; Ml, maxilla; LP, labial palpus; M, mouth opened by dissection; L, labium; O, ocellar field; 1, probably stipes of maxilla; 2, probably cardo of maxilla)

7, First abdominal segment (A) of C. oculata, showing no lateral tubercles, and (B) of C. nigricornis, showing very small lateral tubercles

first abdominal segment has been generally mistaken for a subsegment of the metathorax. There are without doubt ten abdominal segments in all the larvae. The last two segments are somewhat tubular and are retractile, or telescopic.

The dorsal blood vessel is very distinct in all species seen. It extends along the mid-dorsal line from the prothorax to the seventh or the eighth abdominal segment. The vessel is usually black to grayish, or even amber-colored. Pulsations can be readily seen in the middle part.

The pulvillus presents another modification. This is a trumpet-like structure, resembling the so-called "sucker" seen in many of the sarcoptic mites. The larva uses these pulvilli in walking on glass or other smooth surfaces, in which case the pulvilli are bent or twisted as if they were of rubber. It is usually stated that they adhere by suction, but the absence of strong musculature and the irregular border of the arolium appear to be against this view. Furthermore, no trace of any secretion could be seen by repeated observations with magnifications of all powers including an oil-immersion lens. Dewitz (1884 b) held the view that there was a secretion.

The species differ but little in morphology of the larva. The first segment of the abdomen in *Chrysopa nigricornis* has definite small lateral tubercles, while in other species thus far seen the lateral tubercles are very much smaller or are lacking in this first abdominal segment. The other lateral tubercles differ in size in the various species. In *C. rufilabris* they are very small, in *C. plorabunda* they are of medium size, in *C. oculata* they are large. The stalks are short in *C. rufilabris*, medium in the *oculata* group, and very long and slender in the trash carriers (*C. lineaticornis* and others). The trash carriers have also a much shorter and somewhat humped abdomen in comparison with the *oculata* type. The modification of the abdominal setae and tubercles fits the larva admirably for carrying its packet. In *C. cockerelli* there are from one to three rows of microscopic hooked setae on each abdominal segment to the seventh, which assist in holding the packet in position.

There is a difference in the color of the setae from the lateral tubercles. They are all colorless in *C. plorabunda* and *C. quadripunctata*; in *C. nigricornis* all are colorless except the two large central ones, which are black; in *C. oculata* and *C. chi*, all have black bases and the greater number are black throughout. *C. rufilabris* has short, colorless setae, and in *C. oculata* the setae are perhaps as long as in any species seen.

Habits

Where found, and methods of concealment

It is not always easy to find chrysopid larvae. The different species occur in fairly well-defined habitats, and the larvae usually rest extended in crevices of bark, on twigs, on flower clusters, or in rolled leaves. But the somewhat clear body contents of the young larvae blend with the translucent leaves and make the larvae difficult to be seen. Very often they rest on a dead patch in a leaf or in curled-up dried leaves and their predominating reddish color renders them almost indistinguishable.

The most favorable place to search for larvae of *Chrysopa oculata* is on herbage where aphids or young scales are abundant. But even here the larvae are rarely found in numbers. Thirty small larvae of this species were placed on a large stalk of lamb's-quarters which was heavily infested with the black aphids so frequently found on them. The next day a search of five minutes was necessary before the first larva was found. Only three or four were found on the plant, but as many more were found on plants near it.

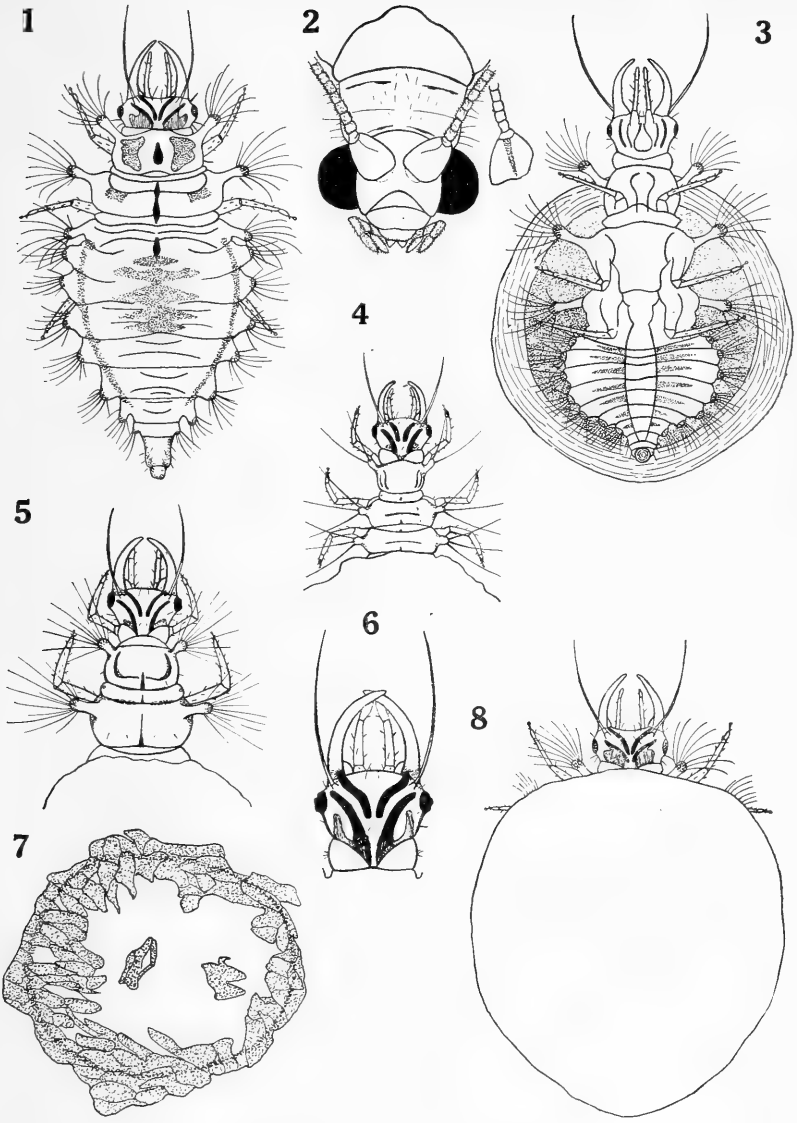
The species frequenting herbaceous plants and shrubs are *C. oculata* with all its varieties (including the two nominal species *chlorophana* and *albicornis), C. rufilabris, C. plorabunda, C. chi* and its variety *upsilon,* and *C. interrupta.* On trees such as the maples that are commonly planted for shade, the chestnut, and the elm, *C. nigricornis, C. rufilabris,* and *C. quadripunctata* are most commonly taken. *C. harrisii* was taken on pine and oak, and *Allochrysa virginica* and *C. lineaticornis* on oak.

Trash-carrying larvae

The trash-carrying larvae of *Chrysopa lineaticornis* have been found on linden trees (on both trunk and leaves), on small oak and hickory saplings, on honeysuckle, and on underbrush in general. They prefer a well-shaded locality. Both *C. bimaculata* and *C. lateralis* were sent to the writer, by state nursery inspectors, from Florida, where they are said to be abundant on citrus trees. *C. cockerelli* larvae were found on the trunks of maple, linden, and apple trees.

The trash carriers build over the abdomen a hollow hemispherical packet.[2] A dorsal view of one of these larvae in most cases reveals no larva at all, but merely a little clump of cottony material, for, when the larva is quiet, the head, the tail, and the legs are drawn in and thus the larva is largely concealed. But when it begins to move, the head and

[2]The word packet is used here because, first, there are many kinds of material brought together, and secondly, the mass is not on the larva's back by accident but is constructed by the larva. It is literally a little pack of debris.



CHRYSOPA LINEATICORNIS

1, Dorsal view of grown third-instar larva, with packet removed; x about 8 1-5
2, Head and prothorax, showing markings; posterior view of antenna showing black line
3, Ventral view of mature larva, with packet in position; x 8 1-5
4, First-instar larva, 5, second-instar larva; x about 10¾
6, Head of third-instar larva, showing third pair of spots
7, Cocoon, showing debris of packet adhering
8, Dorsal view of third-instar larva, with packet in position as in walking; x about 10¾

at least the prothorax protrude anteriorly and the tail protrudes posteriorly (fig. 162, page 1366). The larva walks rapidly and the packet sways from side to side rather unsteadily.

On removal of the packet it will be observed that the larva possesses striking specializations for carrying it. The posterior part is fastened to both the lateral and the dorsal abdominal setae. Rows of minute setae with recurved tips were discovered on the dorsum of the larvae of *C. cockerelli*, and a later study of preserved material of the other trash carriers revealed their presence on these also. In *C. cockerelli* they are more prominent than in the other species, being arranged in from one to three rows across the body from the metathorax to the seventh abdominal segment inclusive. There are as many as thirty of these setae in the longer rows. They are well suited to holding the packet materials securely on the abdomen. The anterior half of the packet is free, but rests on the up-curved, fan-shaped setae of the thoracic tubercles. In addition to the proper support being thus given, the free anterior part permits the larva to stretch out in walking or running. The tail, being free, is extended and so the larva is unhampered in getting about. The abdominal setae are fairly long and the knobs are small. While the abdomen is unusually wide, the segments are narrow, so that the abdomen is shorter and more arched than in other larvae.

The building of the packet is most interesting. The performance may be observed by taking the packet from a larva in a vial, and putting it back into the vial by bits. The larva, with its packet removed, runs around rapidly in evident search of something. With its palpi, antennae, and jaws it seeks from side to side and in every crevice. If a fairly large piece of the packet be dropped into the vial, the larva, touching it, very quickly crawls under it. As soon as the debris is on its back, it is worked backward by the combined efforts of the jaws and a shifting of the abdomen. The head can be bent nearly straight backward when the front pair of legs is lifted, and can be turned to each side for a considerable distance. As soon as the large piece of debris is in place, the larva shifts it from side to side and from the front. A bit of the debris is pulled out and poked back into the pack again. In this way, the material is made more or less solid and the parts are woven into one another to form a firm packet. If more of the debris is added at intervals, it is grasped by the larva's jaws and placed on the anterior border of the packet. It is then worked in and pushed backward, and the straggling ends are picked up and pushed into the packet. Along with the work of the jaws, the abdomen, in a series of wavelike contractions, shifts the packet posteriorly.

Very often the setae, for some reason, catch and hold debris of this nature. Perhaps these setae are more or less viscid. The large cell at the base of each seta has been described as glandular by Lurie (1898), who says furthermore that the setae possess a lumen to the tip. These long setae occur on all larvae, even on species not normally carrying a packet. The dorsal setae are the chief shifting agency. If the abdomen be horizontal and a bit of debris be on the seta, when the abdomen is bowed downward in this region the posterior setae are brought to the packet and will very likely catch into the packet, so that when the abdomen is straightened out the debris will be carried back with the posterior setae. This process takes place in a kind of wavelike shifting, and the packet is actually carried back as far as there are dorsal setae.

After the larva has its packet restored, it remains quiet on a leaf or a twig.

On tearing a packet apart, one finds that it is constructed from bits of debris or small particles of plant tissue which the larva can readily find in its habitat. Insect skins, bits of spiders' webs, egg sacs, the bodies of spiders and mites, bits of wood and bark, lichens, coccid scales and bodies, and insect parts—especially legs, heads, wings (particularly elytra), and antennae—constituted the usual materials of the packets seen. This mass is held together, it appears, by plant fibers, by the silky or cottony secretions of aphids, and by the silk of spiders. The writer found a large amount of such cottony materials accessible to the larvae. Lurie (1898) stated that the packets are bound together by silk spun by the larva. The packets of a few larvae were removed and then returned to the larvae in small pieces. Each larva placed a part of the debris on its back, and gathered up the loose ends and thrust them into the part on its back but did not spin any silk to hold the mass together. The packet is characteristic of all instars, as is true of the Australian species; while silk spinning, in all the larvae observed, is confined to the last part of the third instar.

There are, in literature, statements to the effect that most, if not all, chrysopid larvae put the skins of their victims on their backs as a measure of concealment. The trash carriers are the only ones seen that have this as a well-defined habit. Larvae of *Chrysopa quadripunctata* often carry considerable debris and may appear at times to have this habit, but there is never a well-defined packet present. Larvae of the *oculata* group have frequently been seen with a few aphid skins, or even a number of them, adhering to the setae (Plate LXXXVI, 3). This is to be regarded as accidental, however, or at least as incidental to the larvae's living where there were aphid skins or cottony material, taken with the

fact that the setae are so placed that they readily catch such loose material. Furthermore, it surely is not necessary that larvae be concealed or in any way disguised in order that they may catch insects of such marvelous stupidity as aphids. It is better to interpret this habit as giving security from the larva's enemies, especially birds and hymenopterous parasites, and not as a disguise to assist the larva in catching its food. The trash carriers live almost wholly in the open, as on the branches of trees or the upper sides of leaves. The uncovered species hide in cracks or crevices and in rolled-up leaves which effect similar protection.

Foods

In all species the food of all stages is essentially the same. Very young larvae show a preference for eggs and small aphids or young scales, but they will attack also the larger aphids. Furthermore, if opportunity presents itself, the larvae will attack and kill adults of their own kind. These cannibalistic tendencies, already noted in the case of young larvae, continue throughout the entire larval period. The writer has never observed a larva attack a cocoon and succeed in piercing it. Prepupae and pupae in cocoons appear to be secure from these attacks.

While larvae can thus appropriate their own kind in this manner, their main food consists of small, soft-bodied insects and related forms. Aphids constitute the most important food of all species thus far seen. The larvae of *Chrysopa oculata* ate every kind of aphid given to them. In the main, however, aphids from cabbage, cauliflower, radish, turnips, spiraea, buckthorn, dogwood, maple, chestnut, apple, carnation, chrysanthemum, lily, rose, aster, goldenrod, lamb's-quarters, and nasturtium, were used. All were readily eaten by the larvae. Not all are equally suitable and desirable, however. The most desirable, from all points of view, are the aphids from cabbage, cauliflower (Plate LXXXV, 3), and radish (probably all aphids of the same species), and those from rose. Chrysopid larvae, as well as the adults, attack winged aphids just as readily as they do wingless ones. Where winged forms have been given them alone, they have thrived just as well.

It has been observed frequently that larvae suck up drops of plant juice, and even insert or attempt to insert their jaws into soft plant tissue. Without doubt larvae can derive some sustenance directly from succulent plant tissue.

In addition to eating all kinds of aphids and aphid eggs, the larvae readily attack scale insects. Young scales that have not formed their hard covering are especially suitable for food for chrysopid larvae. If old scales are given to them, they raise the scales or pierce them on the side and suck out the juices. Tower (1915) tells of a Chrysopa larva

which inserted its jaws through the epidermis of a leaf and reached a leaf miner. Walsh and Riley (1868) wrote of a larva which attacked a curculionid larva in a peach. More common are their attacks on small caterpillars, mites, and young or small spiders. Caterpillars larger than chrysopid larvae can ward off the attacks of the larvae by turning the head around or twitching suddenly as soon as touched. Mealy bugs and mites are readily eaten. Small spiders, especially recently hatched ones, are excellent food for young larvae. Marlatt (1895) wrote of attacks of the larvae on the pear psylla. Both adults and nymphs of Psyllidae are readily eaten. Experiments were conducted chiefly with the psyllid species on English ash. A larva of *Chrysopa chi* fed for some time on a much weakened dolichopodid fly.

Chrysopid larvae are not omnivorous. Not all heavily chitinized insects can be pierced by the jaws, and very active insects can be caught only with difficulty. Active larvae, as, for example, fly maggots, frighten away the chrysopid larvae. Coccinellid, chrysomelid, and syrphid larvae, all of which occur in association with chrysopid larvae, are not commonly used for food except perhaps when just hatched.

In the way of artificial foods, beef tea and a weak sugar solution were used. A cotton plug or a piece of absorbent cotton was dipped into the liquid, and the larvae came to the cotton and sucked up the drops. They fed on both these liquids, but whether they could be reared on them was not determined. Both cane-sugar and maple-sugar solutions served successfully for food. The larvae sucked up drops of water also when it was provided.

Larval feeding

The rapidity of feeding, as well as the search for aphids, is somewhat dependent upon how hungry the larva is. When it is very hungry but not weakened, its movements are very agitated and it may even walk over a few aphids without observing them.

After the larva has impaled an aphid, feeding proceeds as follows: The chief movements, as seen from the dorsal side, are the sliding back and forth of the maxillae in the grooves of the mandibles. This is a regular forward-and-backward movement. If both jaws are inserted in the aphid, the two maxillae move together, pulling the labral region backward and forward with it. The aphid is readily turned over and over by spearing it on one jaw, then turning it with the other, and so on, quickly seesawing it back and forth until it is thoroughly exhausted. At the end of the feeding process, the aphid is turned over and over, squeezed out, and finally speared on one jaw. This jaw is moved far outward and the aphid is pushed off the jaw by the tip of the other jaw.

As the larva feeds, the antennae are held almost erect and the labial palpi are held a little forward of straight downward. Undoubtedly in these positions these organs are the least likely to come in contact with the struggling aphid; such contact would either afford some assistance to the aphid in its feeble efforts to get away, or impede the process of turning it over.

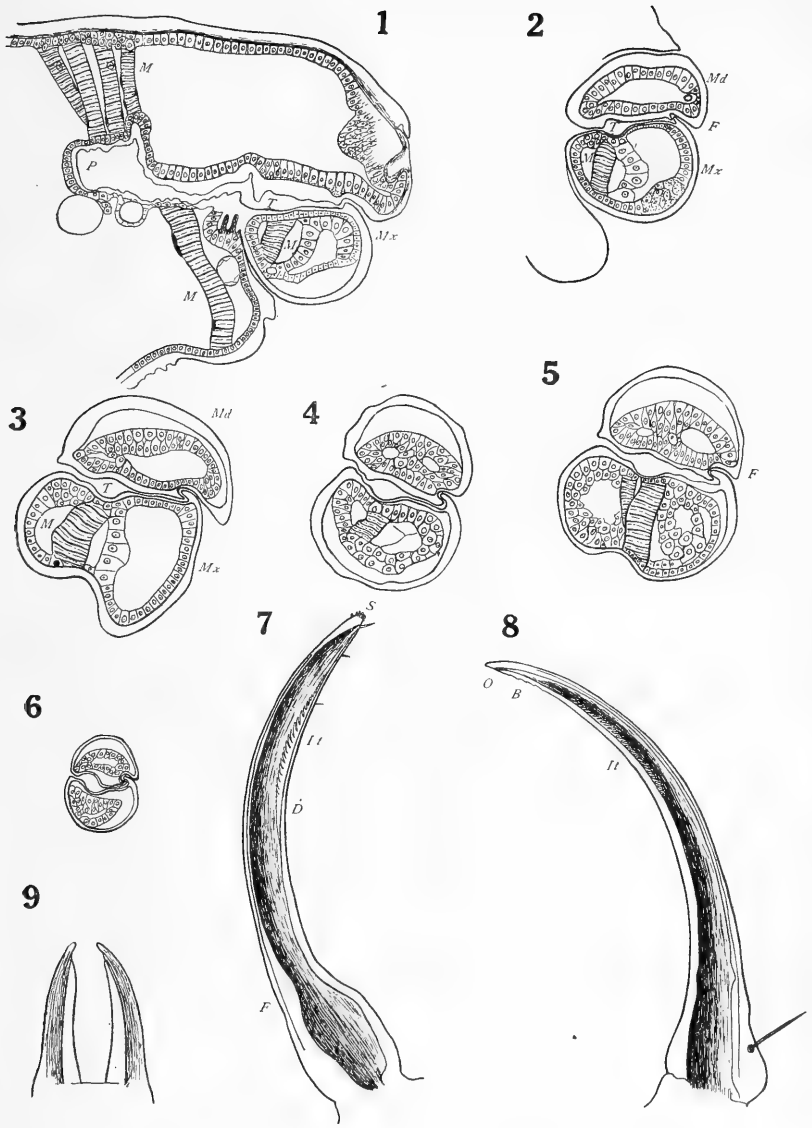
The aphid is nearly always elevated more or less. This is undoubtedly in order to lift the struggling aphid into the air and make its movements futile—not to allow the juices to run down the tubular mouth parts of the larva, as is sometimes stated.

In very young larvae, one can see alternate pharyngeal contractions and expansions near the middle of the head during feeding. This can be observed in newly hatched larvae of *Chrysopa quadripunctata*. Furthermore, if these young larvae are given a small red aphid, a spurt of red juice may be seen flowing into the pharynx with each backward pull on the maxillae. The stream of juices flowing up the tubular mouth parts may be observed also in grown larvae. At the beginning of the feeding, there is generally an uninterrupted stream up each mandible; but as the aphid nears exhaustion, the streams are broken by air bubbles so that their rate of travel up the tubes may be readily observed. When the maxillae are pulled back, these bubbles fly up the tubes very rapidly. At the end of the feeding, only an occasional drop is obtained.

No evidence of the injection of any fluids into the body of the aphid has been observed. The maxillary movement may serve in part to assist in breaking down internal tissues, as these tissues are completely disintegrated, leaving little more than the chitinous parts to be cast aside.

On the ventral side of the head there is more movement visible than on the dorsal. The entire venter of the head, the labium, and the labial palpi, move back and forth with the maxillae. This movement is most evident in the region of the bases of the labial palpi. If only one mandible is inserted, the movement is confined to that side of the venter. The rapidity with which the larva can shift the sucking from one side to the other is striking. First it sucks with one jaw, then with the other, and then with both, more quickly than can be timed.

The muscular action which enables the larva to suck up liquids can be understood by a study of cross sections (Plate LXXVII; also Lurie, 1898). There is a prominent muscle extending from the floor of the maxilla to its upper wall, being attached just beneath the depression that forms the lower part of the sucking tube. This strong muscle is present in all sections from the bases of the maxillae to very near the tips. There is another prominent muscle from the tubular connection of the jaws to



MOUTH PARTS OF CHRYSOPA OCULATA, GREATLY ENLARGED

1, Section through head at connection of pharynx with left jaw (P, pharynx; T, tube between maxilla and mandible; M, muscle; Mx maxilla)
2, Section of jaws beyond head (Md, mandible; Mx, maxilla; F, chitinous flange holding jaws together)
3, 5, 4, 6, In order named, sections of left jaw at intervals toward tip
7, Inner view of left maxilla of a mature larva (S, sensory papillae; It, internal teeth; D, semi-tubular depression; F, flange)
8, Inner view of left mandible. In life this fits above maxilla shown in no. 6. (O, opening into semi-tube; B, apical teeth; It, internal teeth)
9, Jaws of a hemerobiid larva, shown for comparison

the floor of the pharynx. But the most striking musculature is about the pharynx. There is a series of muscles from the pharynx to the dorsum and the venter of the head, as well as to the arms of the tentorium. When these pharyngeal muscles are contracted, the lumen of the pharynx is increased and the juices are sucked up by a typical sucking action. But the muscles in the maxillae also contract and assist the pharyngeal muscles in their work. The opening at the tip of each jaw is single, and is formed by a curvature in both and not in the maxilla alone. The mandibles are sharp at their tips and constitute the piercing agency.

The number of aphids that a larva may eat at one feeding depends, of course, on when it was last fed, on the size of the aphids, and on the size of the larva. A hungry third-instar larva will eat ten cabbage aphids in rapid succession. From ten to twenty larger aphids usually suffice for a day's supply, though more were usually given.

From hatching to pupation, a larva may devour from ninety to two hundred and fifty aphids, depending on their size. The following table is an accurate count of the number of aphids consumed by three larvae of *C. oculata*, by instars, from hatching to spinning:

	Date hatched	Date of first molt	Date of second molt	Date of spinning	Total number of aphids eaten
Larva No. 1	June 1	June 7	June 13	June 18	
Number of aphids eaten, by instars		38	48	68	154
Larva No. 2	June 1	June 7	June 13	June 23	
Number of aphids eaten, by instars		35	68	99	202
Larva No. 3	June 1	June 7	June 14	June 19	
Number of aphids eaten, by instars		46	60	50	156
Average number of aphids eaten by each larva					171

Buckthorn and spiraea aphids were used in this test, and a special effort was made to get aphids of uniform size. At another time a more extensive count was made, using 22 larvae and rearing them through to spinning. In this case 3036 aphids were required, or an average of 138 to each larva. The rather large black aphids on lamb's-quarters *(Chenopodium album)* were used for this test.

Anal proleg of larva

The anal proleg, or tail, is used to excellent advantage by the larva throughout its whole life. It is always used in locomotion except when the larva is running very fast. Then it is either merely lifted from the surface or extended horizontally. In the former case, the abdomen is curved and the end is held just above the surface on which the larva is running. This condition prevails when there is a possibility of the

larva's falling, as in climbing up on the side of a jar or a plant. It is the safety agency in the larva's descent along the stalk after hatching, and it is the larva's main dependence for surety in climbing up and down plants, twigs, glass, and the like. It is used also to brace the body when the larva is handling a struggling aphid.

Reference has been made to a disklike ending of the abdomen. This disk is applied to the supporting surface, and a sticky or gelatinous substance is exuded which enables it to hold fast. At first observation it may appear that the larva holds fast by suction, as stated by Fitch (1855). If a larva be allowed to walk over a fresh, green, smooth leaf, and the highest-power binocular objective be directed upon the tail and the spots covered by it, the little disks of viscous fluid, more or less complete, can be seen on the leaf. It can also be readily seen that the end of the abdomen is immersed in a drop of this clear liquid.

Larval excrement

There is no voidance of larval excrement. It has been known for a long time that the mid-intestine is closed behind (Lurie, 1898, and McDunnough, 1909), and the excrement is stored up in a bean-shaped mass throughout the life of the larva. The darkened appearance of the anterior part of the abdomen is generally due to this black mass within. It is rather surprising that the mass from the entire larval life is so small, but the explanation lies in the fact that the food is liquid and the amount of residue is small.

Classification of larvae

The first basis for classification of the larvae is the marks on the head. These serve to class the larvae into groups which for the most part appear to be most closely related as adults. After the head marks, the general coloration of the body is used. The color of the metathorax varies in the different species. The color of the margins of the thorax and the abdomen are often specific. The first abdominal tubercles differ slightly as to their degree of development. The following key is for third-instar larvae:

A. Two prominent, black, elongate spots on dorsum of head.
  B. Spots extending longitudinally, converging posteriorly.
    C. Jaws amber-colored; legs with smoky or darker patches on femora, but not predominantly dark.
      D. Body of larva brick red or darker above; without a wide gray border on each side of dorsal vessel; yellowish border each side of abdomen; thorax with a prominent yellowish spot around base of each lateral tubercle.....*C. rufilabris* Burm.

DD. Body of larva a more faded red or flesh-colored; a rather large and prominent area of gray on each side of dorsal vessel, leaving a rather narrow dorso-median color area; lateral tubercles of medium size and entirely yellowish or gray..... ..... *C. plorabunda* Fitch

CC. Jaws and legs predominantly smoky to black; lateral tubercles small, yellowish; abdominal tubercles 2 to 4 inclusive marked with reddish..... *C. harrisii* Fitch

BB. Spots transverse; anterior one connecting the two jaws, posterior one the two antennae. Larva a trash carrier. Thoracic tubercles much elongated, setae curving upward; abdomen shortened, and bearing a hemispherical packet of debris capable of concealing the larva..... ..... *C. bimaculata* McClend.

AA. More than two prominent spots on dorsum of head.

B. Three separate triangular spots on dorsum of head.

C. Metathoracic lateral tubercles reddish, brownish, conspicuously darkened, or black.

D. First abdominal segment having at each side a small tubercle which bears short white setae; second pair of abdominal tubercles gray, often with a trace of bright red; bright red spots on each side of dorsal blood vessel in gray borders of same..... *C. nigricornis* Burm.

DD. First abdominal segment without well-developed tubercles at each side; all abdominal tubercles gray, making a gray border on each side; dorsum of abdomen dark brown or brownish black..... *C. chi* Fitch

CC. Metathoracic tubercles gray or yellowish, in some cases with a small band of reddish above but never conspicuously dark; first abdominal segment without definite lateral tubercles; second pair of abdominal tubercles conspicuously darkened or entirely reddish brown; other abdominal tubercles with slender spot of reddish brown above..... *C. oculata* Say

BB. Four elongate prominent black or reddish black spots on dorsum of head, arranged in two pairs of similar spots; often a suggestion of a third pair by the doubling anterior of outer pair toward the eyes.

C. Abdomen conspicuously short, broad, and somewhat arched, about as long as head and thorax combined; lateral thoracic tubercles unusually long and slender. Larvae trash carriers, normally carrying a hemispherical packet of debris.

D. Inner pair of dorsal head spots stopping near middle of head.

E. Mid-western species; inner pair of head spots confluent behind; area between these spots entirely dark except for narrow grayish area; legs dark; no brown on thorax..... ..... *C. cockerelli* Banks

EE. Eastern species; inner pair of head spots not confluent behind, a distinct grayish triangular area between them; thorax generally with light brownish areas dorsally..... ..... *C. lineaticornis* Fitch

DD. Inner pair of dorsal head spots extending distinctly beyond middle of head; smoky to black posterior and outer spots; southeastern species ..... *C. lateralis* Guér.

CC. Abdomen of the usual type, longer than head and thorax, tapering gradually and regularly posteriorly. Larvae never with well-defined packet of debris, but occasionally with some cottony materials adhering to dorsal setae.

D. Head marks in two pairs, curving outward anteriorly; inner pair V-shaped but not confluent at base; outer pair extending from base of antennae in a sharp inward curve to prothorax; body gray, but marked with brown spots..... *C. quadripunctata* Burm.

DD. Head marks in two pairs but extending straight forward, the two pairs parallel to each other; outer spots twice as large and broad as inner ones; body mainly gray, with prominent black saddle-shaped area on thorax..... *Chrysopa* sp.

The prepupa

After a third-instar larva has reached maturity, it usually seeks a more or less protected place and spins a cocoon of white silk in which it transforms to a pupa. One cannot always tell by the appearance of a larva whether or not it will spin soon. Usually just before spinning, the larva engorges itself by devouring a larger number of aphids than usual and then becomes sluggish. It grows rather broad and usually appears to be somewhat flattened (Plates LXXXII and LXXXVI). The term *prepupa* is used to designate that part of the life stages beginning with the first spinning of silk and lasting until the molt to the pupa.

Location of the cocoon

In the open, the larvae spin on the under side of leaves, at the overturned margins or tips of leaves (Plate LXXXVIII, 4), under roughened bark, in flower clusters, or under loose earth. In vials they usually spin under leaves, twigs, or a mass of aphid skins, near the cotton plug, or on the bottom of the vial. Observations indicate that the greater number go to the bottom of the vial to spin.

It was found that larvae of *Chrysopa oculata* may spin their cocoons just beneath the surface of the earth in pot cages. In nature, cocoons of this species are not commonly found on plants. It is thought that they may go below the surface of loose soil and spin, which would account for their scarcity. The earth and sand adhere to the cocoon and make them quite inconspicuous. Cameron (1913) found that *C. vulgaris* also often pupates below the surface of the ground.

Spinning the cocoon

The early part of the spinning can be readily observed, but the latter part is difficult to see since the cocoon is only slightly trans-

parent. If a larva has been observed as having just started to spin, it may be removed to a glass slide or placed in a cell slide, and after some restlessness it will usually begin to spin a new cocoon. In this way the actual start can be seen. A larva spinning on the bottom of a vial, in the angle, first makes a framework by attaching viscid silk thread from the side of the vial to the bottom. The spinning is done entirely by the tail, which, as previously noted, can be extended and retracted in a remarkable manner. The colorless, gelatinous, silky secretion issues from the anal opening in the center of the tenth segment. The larva lies on its back or on one side, and reaches with its tail in all directions. When the secretion touches the glass, the soft silk readily adheres, forming interesting attachment disks. Then the abdomen is moved over to another place and the silken thread issues as it moves from one place to another. The thread is fastened again, and so the process goes on if supports are located.

But if supports for the thread are not found, the tail searches aimlessly about. Sometimes it seeks in vain and may attach a thread to one of its own setae. The tail can be brought forward over the head of the larva and attach a thread, or it can be twisted to either side to a relatively considerable distance. If no supports are available, the threads are fastened on one side of the larva and then carried up and fastened to a seta, or carried over to the other side and fastened. During the first few hours the spinning proceeds rather slowly, and the more so if much time has been wasted by the larva in seeking places to attach the thread. The larva spins for a few minutes in one position and then shifts and continues in the new position. Threads are attached to other threads and by constantly shifting to a new position the larva keeps the cocoon spherical.

The spinning from thread to thread is carried on in a fairly regular triangular design. The shifting continues at intervals, but instead of shifting in a true circle the larva moves to one side a little, and in this way the wall of the cocoon is made of the same thickness. As the larva shifts, the prominent dorsal and lateral setae are broken off and go into the construction of the cocoon. Perhaps these add a degree of strength and rigidity, like the ribs of a basket. Long before the larva is hidden from view it is without setae.

The spinning continues without cessation day or night unless the larva is disturbed. The triangular design continues until the cocoon is at least half completed. Observation from this stage on is difficult, as the larva is partly hidden. There appears to be a fairly gradual change to a figure-8 pattern. The end of the spinning appears to be a general plastering over the inside of the cocoon, which completely hides the

larva from view. This last act is carried out very slowly. Spinning usually requires from twenty-four to forty-eight hours, though some larvae apparently finish in a shorter time.

Special effort was made to see whether the lid, by way of which the pupa leaves the cocoon, was spun into the cocoon. But to date this has not been seen, nor have any constant characteristics in the spinning process been observed which would warrant the conclusion that it was spun into the cocoon by the larva.

If, while a larva is spinning, the cocoon be torn or the outside be pressed in with a dissecting needle, interesting reactions follow. The larva tries to defend itself and may plunge its jaws through the unfinished cocoon in this effort. Spinning stops for the time being. After a short period of waiting, the jaws are withdrawn and the spinning proceeds. If the cocoon be cut or torn, the opening is patched so that at the end the tear can scarcely be found. It is made of the same thickness as the remainder of the cocoon.

If a spining larva is disturbed, it does one of two things: it either walks around for a while and begins to spin at another place, or goes to the bottom of the vial, coils up, and spends its pupal life outside the cocoon. Disturbed larvae have been observed to come back to the cocoon first begun and spin another beside it. If the first cocoon is well started, the chances are that the larva will not spin further, since, as Lurie (1898) pointed out, the amount of silk secretion is undoubtedly limited, and if too much silk has been wasted in an unsuccessful attempt to form a cocoon the larva cannot secrete enough to complete another. It may, however, spin feebly for about twenty-four hours, making a mat of silk around the tail. A very few larvae appear to make no attempt at all to spin, but pupate in the open.

The cocoon

The cocoon is spherical or slightly elongated in shape (Plates LXXXVII and LXXXVIII), and in all cases pure white in color. The cocoon proper is very thin. It appears like paper, but the original framework gives it more or less of a shaggy appearance. The silky layer is thin, hard, and difficult to tear. It was found, by submerging cocoons for different periods of time, that they could be submerged for several hours without being permeated by water; after a longer time, however, the water did enter. In some cases the cocoon has one or more ringlike bulges. The size of the cocoons varies somewhat in the species, very probably with the size of the larvae that spin them. One cannot with any certainty distinguish the species by the cocoon. The packet-carrying larvae use

their packets as a framework for their cocoons, the debris adhering to the cocoon. The setae to which the debris is fastened evidently break off early in the spinning, permitting the larva to shift its position.

There are two stages in the cocoon—the last part of the prepupal period, and the greater part of the pupal life. The prepupa in the cocoon is doubled ventrad, the tip of the tail lying on the anterior dorsum of the head. It is inactive, but is capable of a little movement. The distinctive colors of the larva largely disappear, but one can usually identify it even after the fading is well advanced. Just before molting, it is often impossible to name the species with certainty. When opened, the prepupa is seen to be filled with a grayish to yellowish white semi-fluid substance, but in the abdomen there is a large, solid, black, bean-shaped body. This is the larval excrement which was packed at the end of the mid-intestine during the larval life. It remains here during the tissue-reforming process through the pupal stage, and the intestine of the adult forms about it.

THE PUPA

The pupa, as it pushes off the old larval skin, is delicate gray to yellowish in color. The eyes are grayish, with small spots of brown. At the center of the base of each eye is a prominent opening, or foramen. The antennae are white or colorless, and are folded over the dorsum of the head, above the eyes, around somewhat to the sides of the thorax, then in an irregular S-like loop over the wing pads, ending behind the wings and somewhat under the body. The most prominent part of the head is the mandibles, which are the most distinctive development of the pupal life. They are relatively large, toothed, and heavily chitinized. Their only movement is as a pair of pincers. There is a prominent labrum. The maxilla and the labium are much reduced but they give a suggestion of the future functional mouth parts. The segments of the palpi, as well as those of the antennae, appear like so many glassy beads. They are incapable of movement. The head is inclined ventrad and its only movement is a slight raising and lowering. The last segment of each tarsus is broadened at the tip, and at each outer angle a very small claw is borne. The wings appear as two pairs of rather prominent pads on the meso- and the metathorax.

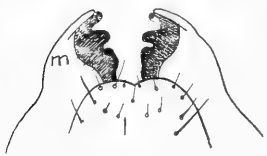


FIG. 157. PUPAL MANDIBLES (m) AND LABRUM OF CHRYSOPA OCULATA, X 32. DORSAL VIEW

Color changes and later development

As the pupa develops, the body changes to a distinct bright green. The head, however, retains the yellowish color in most species. The eyes change from a gray to a deep reddish black. As the eyes develop, the retinulae are outlined by little circles of brown pigment forming regular geometrical figures. If these figures be examined under high power, they will be seen to consist of seven rhabdom cells outlined in pigment, with a small, clear, central area. This offers an excellent opportunity to study the gradual deposition of pigment in the developing compound eye.

In the early pupal stage, the head is unmarked, but gradually the head coloration of the adult appears. *Chrysopa oculata* shows very strikingly the dark bands and loops, but *C. nigricornis* does not show the two labral dots at first. These are developments in the early adult. The basal part of the legs becomes light green, while the tarsi remain grayish to translucent. The legs of the adult can be seen developing within the pupal legs, at first faintly but later very plainly. The developing antennae of the adult may also be thus seen. The wings, continuing their growth, soon fill the pupal pads. They then double up, forming regular loops back and forth. This explains how the large wings of the adult can develop in such small pads and be pulled from the pads so easily. As soon as this folding occurs, the tracheation and venation are obscured. The hairs on the wings show clearly and obscure most of the wing surface.

These developmental changes can be followed by the external appearance of the cocoon. As the color of the larva fades to yellowish or gray, the cocoon takes on a tint of the same color. The cocoon, as a whole or in spots, at least after pupation of the larva, has a greenish tinge. In cocoons containing nearly mature pupae, the eyes can often be seen as two dark spots. When these eye spots are the darkest, the green color the most noticeable, and the black disk the most evident, the pupa may be expected to emerge.

Cocoons that were wholly black were sometimes found. This generally indicated that the prepupae within were dead, often parasitized. In cities, black or very dark cocoons were frequently found on trees, but some of these had been discolored by soot or smoke. Fungous growths on a cocoon have been observed to be positive evidence of the death of the pupa or the prepupa.

Length of pupal life

The shortest periods of time from spinning to pupation in the different species was from three days to twelve days. Records of from ten to twenty days were more frequent than earlier ones. In overwintering generations, which remain in the cocoon as prepupae, this molt does not occur for a period of from four to eight months. The pupae emerged from the cocoon in a minimum of five days after pupation. This gives a minimum of eight days in these rearings for the length of pupal life. Records of from twelve to twenty-five days, however, were more frequent. Development was most rapid in midsummer.

Emergence of the pupa

When the pupa has matured, it leaves the cocoon through a circular opening at one end. This opening is generally directly opposite the black disk, though in rare cases this disk, which is the molt, may be located on the side. The pupa, by exerting sufficient upward pressure, causes the end to tear in the form of a circular lid, which was observed in all cases to be hinged by at least a few threads.

A question has arisen as to the exact manner in which this lid is formed. Some writers state that it is spun into the cocoon, others that it is cut free from the cocoon by the large pupal mandibles, and still others that it is torn by upward pressure. The writer has not observed anything at spinning that might be interpreted as the formation of this lid in any species. If it were cut by the mandibles, it appears that the edges might be jagged and somewhat irregular, yet this is not the case. Furthermore, cocoons would occasionally be found with the jaws protruding in the act of cutting the lid, yet this has been neither seen nor reported.

The writer is not definitely convinced as to the correct explanation. It appears most likely to be a combination of the above explanations. The cocoon is so constructed that, when a rent is started, it tears in a circle with clean edges. Near the ends, one can tear off a lid; near the middle, however, the ends of the tear do not meet, but a narrow strip like a continuous apple peel results. Therefore the manner of spinning may account for the end tearing in the form of a lid.

It has been repeatedly observed through the thinner cocoons, as of *Chrysopa rufilabris* and *C. plorabunda,* that the pupa is able to shift its position with surprising rapidity. This can be demonstrated by exerting a little pressure on the exterior of the cocoon. The pupae have been observed to turn quickly to avoid injury. By raising its head slightly, a pupa can bring pressure to bear on the upper end of the

cocoon. It is possible that by the shifting about of the pupa in the cocoon, some area is weakened, so that when the pressure is exerted the rent begins. However, no observations have been made substantiating this theory. After the rent has been once started, the further pressure and emergence of the pupa causes it to broaden to almost a circle.

Once out of the cocoon, the pupa must molt before it becomes an adult. This molt was the critical period in reared Chrysopidae; the fatality in these rearings was at first between thirty and sixty per cent. It was observed that as soon as the pupa had emerged, it walked around on the bottom of the vial and sought repeatedly to climb up the sides. When twigs or leaves were placed in the vial, the pupa climbed up at once, holding on with its claws and occasionally using its jaws to assist it. After hastily investigating the leaf or twig, the pupa braced its legs and began the stretching and expanding process which makes possible the splitting of the pupal skin. The providing of materials enabling the pupae to climb and properly orient themselves greatly reduced fatalities. If suitable supports are not found, the pupae may not be able to molt, but may grow weaker and more inactive and finally die. A weakened pupa rarely succeeds in shedding the pupal skin, as the process is a strenuous one, requiring all the strength that the most active pupa can exert. Pupae may also be removed to plants, where the molt can take place under natural conditions.

The pupal molt

The shedding of the pupal skin corresponds very closely to a larval molt. The writer has frequently watched pupae shed their skins, under a lens, and one instance, that of a female of *Chrysopa oculata,* may be described as a typical case.

The pupa emerged from the cocoon and was taken from the vial and placed on a plant. It walked around over the leaves excitedly, and thus investigated several leaves. Finally it took up its position near the end of a stem. It braced its legs and began to inflate or expand itself by a series of regular movements simulating breathing. Numerous writers have commented on the phenomenon of so large an insect coming from such a small cocoon; in fact, the size of the expanded pupa is several times the size of the cocoon. The abdomen is extended to the normal adult length. The thorax also is expanded. There is considerable muscular movement during this expansion. The abdomen is raised and lowered, and extended and contracted, alternately. The head is raised and lowered. This pupa continued the expansion for ten minutes. It rested for perhaps a minute, and then a series of movements, calculated to shift the abdomen forward, was begun. The abdomen and the thorax

moved forward within the pupal skin, leaving it behind. The inevitable consequence was the stretching of the pupal skin in the anterior region. This continued until a rent started. There has been some difference of opinion as to just where the tear occurs. In this instance, it began over the occiput of the head and was rapidly extended back over the prothorax by a few further shifts. Bending the head caudoventrad, the pupa first carefully freed its mouth parts. It pulled upward and worked the mouth parts constantly. The antennae formed two loops over the front of the head and began at once to slip out of the old pupal skin. The pupa pulled upward slowly and deliberately on the mouth parts, continuing to move them in and out. Finally they slipped off, revealing the bright colors of the head. The pupa then began to straighten up slowly in order to pull out the antennae and the two anterior pairs of legs. The antennae were guided upward by the maxillae. These were spread apart and they grasped the antennae in the withdrawing process. The metathoracic coxae may also assist in the withdrawing of the antennae by being moved forward and pushing the antennae outward.

The pupal skin remained attached throughout this performance. The pulling upward continued until the pupa appeared to be supported only by the abdomen. Finally the front legs were freed, followed by the second pair. At about the same time the antennae were free and sprang into place. During this performance the wings were pulled from their pads. As the adult lifted itself upward, the chitinous linings of the tracheae were pulled out. With the freeing of the anterior part of the body, the pupa, having the first two pairs of legs free, walked slowly ahead, thereby pulling out the metathoracic legs, the remainder of the wings, and the end of the abdomen.

The pupal skin remained attached as a hyaline molt, retaining its former shape but with a large rent above and possessing no characters by which the species could be determined. Two long, slender claws at the end of each tarsus could be seen, but the pulvillus was not well defined.

Very little variation from the foregoing account has been observed in the different species studied. In *C. nigricornis* the rent was observed to be started at the border between the meso- and the prothorax. It then extended forward to the head, and continued to the eyes in the form of a Y. The whole process, from the beginning of the expansion to the time when the adult walks away, requires from fifteen to twenty minutes.

THE ADULT

Expansion of the wings and darkening of the veins

The imago generally walks about excitedly for a few seconds, going a short distance and then coming to a stop with the end of the abdomen downward. This position facilitates the spreading of the wings. If the supporting surface be turned upside down repeatedly, the imago will just as often assume its first position. The wings expand presumably by blood pressure, the expansion beginning at the base and extending outward. The tips are the last to expand, usually requiring a half hour before being fully expanded.

The veins and veinlets of the wings are wholly green at first, but certain ones soon begin to darken, first at the basal part of the wings and lastly at the outer parts. The adults of *Chrysopa oculata* exhibit a variation in this respect, from entirely green to fairly dark. A series may readily be arranged, including perhaps twenty individuals, with a gradual succession of changes in the extent of pigmentation of the veins. *C. nigricornis* also shows considerable variation. The first veins to darken are the gradate series, between the branches of the radius. The costal veinlets and the ends of the branches darken next. The base of M_{3+4} (the divisory veinlet) has not been observed to be a true index to the degree of darkening of the wing.

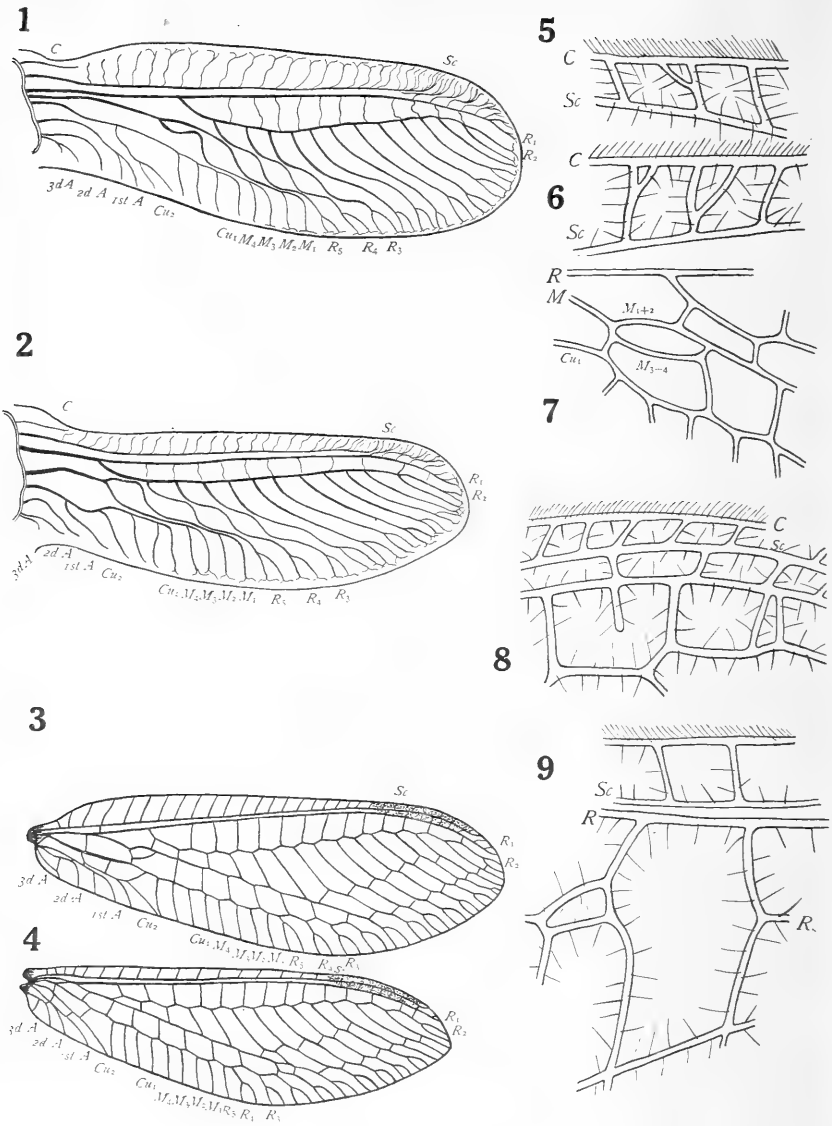
Voidance of larval excrement

The black mass of larval excrement which was seen near the end of the abdomen of the pupa, and which, in the newly emerged adult, can be readily located, still must be voided. The voidance appears to require considerable effort, and is accomplished from five to fifteen minutes after the wings are expanded.

Tracheation

Pupal tracheation

The camera-lucida drawings of the pupal tracheation (Plate LXXVIII) show clearly its essential points. The costal trachea appears as a very short and rather indistinct trachea at the usual place. It has been overlooked by other workers, but in the course of these studies it has been seen repeatedly in *Chrysopa oculata* and *C. nigricornis*. The branch M_1 is so close to R_5 that it appears to be a part of the latter. Tillyard (1916-17) has so interpreted it in *C. signata*, but in both *C. oculata* and *C. nigricornis* it is clearly a medial branch. A similar condition exists in the cubital region. The outer branch of the cubitus appears super-



WING VENATION

1, Front wing, 2, hind wing, of early pupa of Chrysopa oculata, x about 10¾
3, Front wing, 4, hind wing, of C. nigricornis
5, Branching in subcostal veinlet of wing of C. oculata. 6, Branching in subcostal veinlet of another wing of C. oculata. Both x about 18
7, Unusual fusion of M_{3+4} with M_{1+2} in wing of C. oculata. The so-called divisory veinlet is here very similar to that in Allochrysa)
8. Accessory veins between R1 and Rs in region of stigma of C. oculata, x about 18
9, Dropping-out of Rs in hind wing in C. oculata, x about 18

ficially to be a branch of the media. This branch sends three smaller branches to the outer margin. The fourth branch basad is Cu_2. There are usually only three anal tracheae, but in several instances a minute fourth was seen. There appears to be some variation in the second and third anals. These tracheae are small and difficult to study, but the essential features are fairly clear. The tracheation of the hind wing is almost identical with that of the fore wing.

Application of tracheation to wings of adults

It is evident that a correct interpretation of the venation of the adult Chrysopidae is impossible without a previous understanding of the pupal tracheation. The modifications shown are peculiar to the family, so far as is known. The first modification is seen at the tip of *Sc*. In the pupal wing, *Sc* ends at the inner border of the stigma. In the adult wing it appears to end beyond the stigma and near the tip of the wing. The stigmal cross-veinlets are the fused branches shown in the pupal wing from R_1. There are few cross-veins between *Sc* and *Rs*, and these are at the extremities. This condition enables a kind of rotation to take place in flight, for both the cutting edge of the wing and the flexible hind border. The radial sectors in both pairs of wings of the adult are zigzagged, while in the pupal wings they are straight tracheae.

It is at the end of the radial system and throughout the medial and cubital systems that the greatest coalescence occurs. The best way to name these branches is to find Cu_2, which corresponds to that branch in the pupal wing. It arises rather far basad from Cu_1, and is branched in the front wing and unbranched in the hind wing. This vein having been found, the fourth branch forward is Cu_1 in both wings. Then, in regular sequence forward, the veins are M_4, M_3, M_2, and M_1. It will be observed that in both front and hind wings this arrangement generally holds, stopping with the fork of R_5. In either wing, however, some variation occurs in this region. M_1 and M_2, and M_3 and M_4, may be joined at their bases and simulate the branched R_5. M_1 may also be branched like R_5.

The branches having been named, they can be traced to their origin. The ninth radial branch from *Rs* is the last to go straight to the margin without fusions. The tenth to the fourteenth branches, inclusive, so fuse at their bends as to form the pseudo-media and the pseudo-cubitus. *M* is fused with *R* at the base. In the front wing it divides into two branches which fuse quickly, forming the median loop and then separating. Apparently there may be considerable variation in the median loop. The lower branch, M_{3+4}, shifts along the upper branch and may

even fail to fuse with it, as shown in Plate LXXVIII, 7. In such a case a very evident specimen of *Chrysopa oculata* might be placed in the genus *Allochrysa* by existing keys. A specimen of *C. rufilabris* was observed to entirely lack a median loop in one wing. But these variations are unusual, and in the great majority of specimens the wing-venational characters used by Banks and others in keys may be relied upon.

In both wings, *Cu* arises as a separate vein. Soon after its origin in the front wing, a marked thickening occurs. There is nothing in the pupal tracheation that explains it. Cu_2 arises at this thickening and runs toward the margin, but branches slightly beyond half the distance to the margin. The main vein continues forward and gives off four branches to *C*, the anterior of which becomes Cu_1. This differs from Tillyard's interpretation, in that he has shown only three branches from the anterior branch of *Cu* to the margin, compensating by calling R_5 three-branched at the tip.

The short crossveins connecting the radial branches have been designated as gradate veinlets. The various genera differ as to whether there is one or two series present, and also as to the number in each series.

Foods

There has been some difference of opinion expressed in the literature on the Chrysopidae as to whether or not they take food. From the beginning of these studies, *Chrysopa oculata, C. nigricornis, C. rufilabris, C. quadripunctata,* and *C. chi,* were fed plant lice daily, which they ate very readily. The first two species listed were observed to eat them in their natural habitats. Any small aphids, young scales, and mites that happened to be available were given the chrysopids, and were readily eaten though not all were equally suitable in rearing work. A hungry adult of *C. oculata* was observed to devour seven cabbage aphids in succession. All adults apparently relished some water daily also. On the other hand, *C. plorabunda* was never observed to devour live aphids, though this species fed freely upon fluids of crushed aphids, weak sugar water, and plain water. Similar observations were made with *C. harrisii, C. lineaticornis,* and *Allochrysa virginica.* While these were offered various aphids, they were observed to feed only upon sugar water and water. It is thought that the proper food was not discovered, or that the insects may have fed during the night, rather than that they normally took no food.

It can be readily observed that adults depend largely on tactile sensations, rather than on sight, to locate their food. The palpi are

largely used for this purpose. Aphid skins and dead aphids call forth responses similar to those called by live aphids. When the live aphids are encountered, their movements are readily detected, and then they are quickly seized and devoured.

Flight

The flight of the adult is slow, heavy, and rather awkward. The wings are large and the body is comparatively heavy. In the sun, the light is reflected by the wings but the usual color impression is green. Although the flight of the chrysopids is distinctive, they are frequently confused with some Plecoptera (especially Chloroperla), Mecoptera, Hemerobiidae, and the smaller Lepidoptera.

Activity of adults

The inactivity of the adults during the day has been commented on by many writers from Réaumur to the present time. The insects prefer to remain quiet on trees, shrubs, and herbs, during the day, and fly chiefly in the morning and evening. They sit probably most often on the under side of the leaves. Sweeping and beating are the most successful means of taking them during the day.

At Ithaca and at Milwaukee the greatest activity was manifested in the evening, as was evidenced by the attraction of the adults to the electric lights, especially arc lights. It was found that a better collection could be taken here in a few hours on a favorable evening than in several days of sweeping. The activity of the adults begins early in the evening, perhaps at seven o'clock in summer, and their numbers increase until about nine or ten o'clock. The greatest numbers of adults on the wing have been observed on warm, still summer evenings. If a rain be nearing, the conditions are still more favorable. In Virginia, though frequent watches were made at lights, comparatively small catches resulted and nothing rare was ever taken. Adults are somewhat attracted also to sugar put out for moths at night.

Cleaning the antennae and pulvilli

An interesting performance seen frequently in adult chrysopids is the cleaning of the pulvilli and the antennae. The right antenna is cleaned by the right front leg. The tarsus is looped over and the antenna is drawn through the loop. The long hairs on the tarsal segments serve to remove attached debris. The left antenna is cleaned by the left tarsus in the same way.

When an adult attempts to climb up the side of a glass bottle, the pulvilli must evidently be very clean if it is to succeed. The pulvilli are cleaned by the mandibles and the maxillae. The insect picks off adhering particles and apparently bites the pulvillus, probably to increase the flow of adhesive material. All the legs are cleaned by being drawn through the mouth between the maxillae and the labium, the right legs being drawn through the right side of the mouth and the left legs through the left side. There seems to be an adjustment for this in the mouth parts, as there is a definite space, apparently well suited to the purpose, between the maxillae and the labium.

Protective devices

The color of the adults so closely simulates their environment that considerable protection is afforded. But more striking is the repellent odor of most species. This odor is sickening and very objectionable, and has been described as resembling that of human feces. McDunnough (1909) gives a brief account of the glands secreting the fluid that produces this odor. The odor appears to vary in intensity between the individuals of the different species, but it is generally strong in the *oculata* group, in *Chrysopa chi*, and in *C. nigricornis*, and weaker in the *quadripunctata* group. The full strength of the odor may be demonstrated by slightly squeezing the body of an adult between the fingers. A mutilated specimen gives a similar result. The odor will persist on the hands for several hours after adults are handled. This odor is only a partial protection from the insects' enemies, though predacious enemies have been observed to be less serious than parasitic ones.

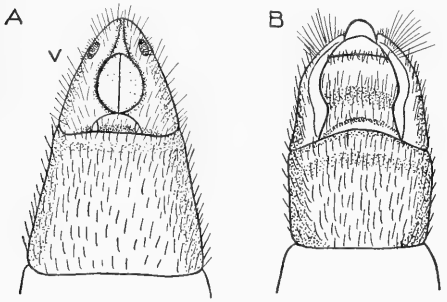


FIG. 158. END OF ABDOMEN IN CHRYSOPA OCULATA, X 8. VENTRAL VIEW

A, In adult female. The two circular areas of peculiar setae are shown, also the genital opening (v)
B, in adult male

The sexes

It was early noticed that the egg-laying females nearly always have very much distended abdomens, due to the eggs contained. So when adults are taken with abdomens larger than normal, it is generally safe to call them females. But the sexes have constant differences in the external genitalia which readily distinguish them.

The end of the abdomen of a female of *Chrysopa oculata* is

seen to be made up of two prominent side lobes, which meet at their posterior extremity but are separated anteriorly (fig. 158, A). The very prominent oblong vulva is located between these lobes, at their base. It has a sharply defined border and is not covered with the prominent hair seen on the lobes. A suture running from in front posteriorly divides it into two equal parts. Both the gelatinous stalk-forming substance and the egg issue from this opening at oviposition.

A ventral view of the end of the abdomen of a male of *C. oculata* shows marked differences from that of the female. The two lateral lobes stop short of the midline and a prominent ventral plate extends between the two borders (fig. 158, B). This ventral plate has a prominent depression extending across it near the middle. There is another lesser depression, parallel to this and a little posterior to it. This ventral plate extends practically as far caudad as the lateral lobes. The genital opening is within the extreme end of the abdomen, above the ventral plate, and the anus opens above it. In side view the abdomen ends squarely, in contrast with that of the female, which has a rounded end, the dorsal part being longer than the ventral. The depressed button-like circular areas bearing the short, peculiar setae occur in the males as well as in the females, one on each side near the dorsum.

Sexual dimorphism

In addition to the genital differences, there is a striking sexual dimorphism in *Meleoma signoretti.* The male develops a prominent frontal horn, which bears a brownish ventral brush of hair (Plate LXXXIV, 6). In the male of *M. slossonae* there is a suggestion of this development and the surface of the front is somewhat irregular, but a definite horn is absent. McLachlan (1883-84) discussed a difference in the width of the costal area of the wings in the two sexes of *Chrysopa flava.*

Copulation

Copulation has never been described for the Chrysopidae. It has been observed several times in *Chrysopa oculata* and *C. nigricornis* during these studies. As a typical case, copulation of *C. oculata* observed under a binocular on June 26, 1916, may be described. About half a dozen pairs of adults of *C. oculata* emerged on June 24. They were put in a battery jar, which was then placed upside down over a small plant infested with aphids. At about 4.30 p. m. on the 26th, several females appeared to be chasing the males about. When they came near each other, both the males and the females began to jerk the abdomen upward

and downward, an act which is generally seen before copulation. The males and the females rubbed their antennae together, and usually the males would fly away. Finally a male and a female continued stroking each other vigorously with their antennae. Then they walked to a position beside each other, facing in the same direction. Then they moved their abdomens together, the male bringing his under that of the female so that the ventral surfaces of the two were together. The male held the abdomen of the female securely. Later they headed in opposite directions. Connection continued for twenty-eight minutes. During this time the only perceptible movements were a slight waving of the antennae and contractions of the abdomens resembling slow peristalsis. Finally the female became restless and started to fly away, but the male held her, even supporting her suspended. After several further efforts by the female to break loose, they separated. Each brought its abdomen forward and appeared to be eating at the genitalia. The male held his genitalia open for five or ten minutes after copulation.

All other cases of copulation observed also occurred at about four or five o'clock in the afternoon. A pair of *C. nigricornis* copulated at least twice. They emerged on successive days and were put together immediately. The female laid about two dozen eggs, which hatched. After these eggs were laid the insects were found in copulation. The beginning of the copulation was not observed, but the insects remained in connection for a half hour from the time when they were first observed. After this copulation, several dozen more fertile eggs were laid. The evidence of the first copulation was circumstantial but, since fertile eggs were deposited, it is not likely that the supposition was ungrounded. The second copulation was observed.

Egg-laying after copulation

A number of experiments were carried out to determine the length of time that elapsed after copulation before the first egg was laid. The female whose copulation is described above, began laying eggs the day after copulation. Observations show a varying lapse of time, from a few hours to six days. The females are fertilized generally soon after emergence, but a minimum of three days is required for the eggs to develop. If oogenesis is well advanced, fertile eggs may be deposited very soon after copulation.

It was observed in several instances that in *Chrysopa oculata*, eggs formed when the females were unfertilized. The females deposited a number of unstalked eggs in the vials, as well as some stalked ones which failed to develop embryonically. A female that had deposited unstalked, infertile eggs, after copulation deposited stalked, fertile ones.

Manner of oviposition

The stalked eggs of the Chrysopidae early attracted attention, and the manner of oviposition has been correctly described, at least in the main, by several writers, notably Fitch (1855), Mueller (1872-73 a), Vine (1895), and Girault (1907 a).

Oviposition has been observed many times by the writer both under a hand lens and under a binocular. A female with a much swollen abdomen may be expected to oviposit soon. Furthermore, if a female is seen to have very recently deposited a few eggs, oviposition may generally be observed without a long wait on the part of the observer. There is a constant twitching and contracting of the abdomen preceding oviposition. Rings of contractions run posteriorly, and the abdomen is repeatedly raised and lowered. The female is usually quiet, moving only when disturbed. The vulva becomes more prominent, then it bulges out, and immediately before oviposition it is pushed out to its limit, being then very conspicuous. Finally the abdomen is brought to the substratum once or several times. Then it touches the substratum apparently with more force, and a drop of clear gelatinous substance is exuded. Following this exudation, the abdomen is raised stiffly upward. The gelatinous substance is pulled out in this way into a long, fairly uniform stalk. Immediately the egg appears, micropyle end last, and attaches itself to the stalk. The egg is held for an instant, presumably while the stalk hardens.

It was observed that the egg in many instances was held not by the genitalia but by the small amount of stalk material which adhered to it. When the drop of gelatinous material appeared, the genitalia were immersed in it before it was drawn out. The egg adhered to it and was held for a few seconds. If the abdomen was lowered a trifle, the stalk bent out of line. After the stalk hardened, the adult freed itself from the egg with a little jerk. Some of the gelatinous substance was frequently seen on the eggs.

The females of the less common species refused to oviposit in captivity, though several types of containers and foods were used. It should be pointed out further that some exotic chrysopids normally deposit unstalked eggs, but all of our species thus far studied normally deposit stalked eggs and all oviposit in the manner described.

Abnormalities in oviposition.—Various peculiarities have previously been described as accidents of oviposition. In closely grouped eggs, as are frequently found with *Chrysopa nigricornis,* striking abnormalities may be observed. Most species deposit their eggs singly, but Sharp (1895) reports *C. aspersa* as laying its eggs in groups, each group being supported by a single stalk.

Not infrequently stalks without eggs were found, also a stalk with a small part of an egg on it. A female of *C. nigricornis* which had demonstrated these and other abnormalities was watched one afternoon. Oviposition was repeatedly attempted, though it appeared that the eggs had become lodged. The insect was observed to deposit a half dozen stalks without eggs, also some stalks with small pieces of the chorion on them. She also deposited other pieces of chorion indiscriminately without stalks. She later deposited normal, stalked eggs. She also deposited one stalked egg with an unstalked egg adhering to it (fig. 159, B), and another with a piece of chorion attached to a normally deposited egg. Near the end of her life she deposited a few fertile eggs without stalks.

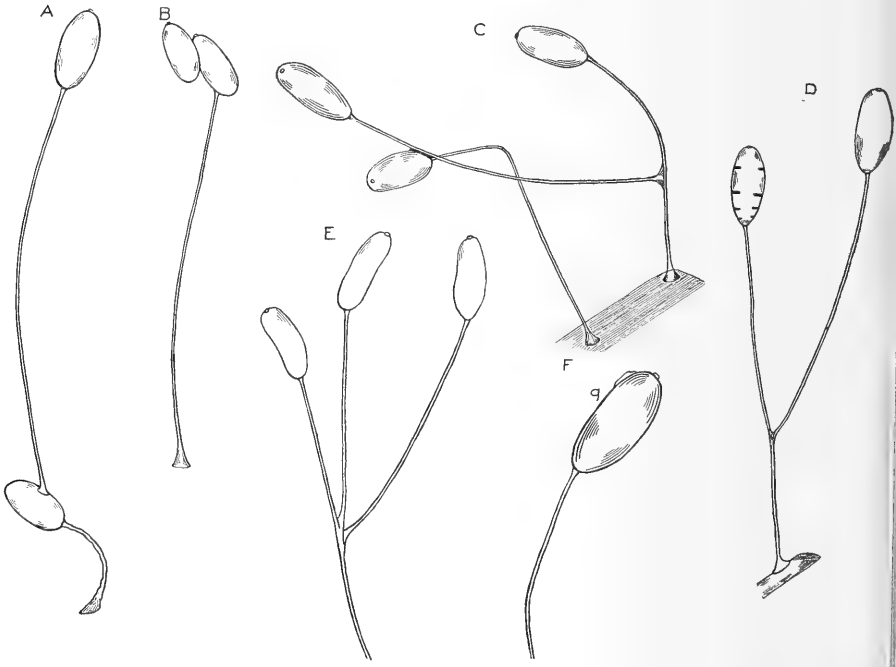


FIG. 159. ABNORMALITIES IN OVIPOSITION

A and B, Abnormal oviposition in Chrysopa nigricornis, x 5¾. C, Accidental fusion of stalks in C. oculata. D, Abnormal oviposition in C. chi. E, Abnormal oviposition in C. oculata. F, Egg of C. oculata showing a drop of the gelatinous stalk material (g)

Length of oviposition period and number of eggs laid.—The usual statements on the length of the egg-laying period are that the adult is short-lived and that oviposition lasts for only a few days. Great variation occurred in rearings, undoubtedly due to the fact that few if any females deposited their full complement of eggs. The largest number of eggs obtained from any one individual was 617, from a female of *Chrysopa oculata* which lived for forty-two days. The second largest number was 470, from a female of the same species which lived for thirty-four days. There was but one copulation in each case and no infertile eggs were noticed. In both cases egg-laying continued up to the day preceding death. Female No. 63 of this same species deposited 326 eggs and then died. On opening the abdomen, 13 nearly mature eggs were seen. Other records in this and other species were in the main smaller than the above numbers, ranging from 294 to 0. The number of eggs that can be deposited is evidently larger than has been previously reported.

Length of life

There is considerable variation in the length of life of different individuals. During an attempt to winter adults, a female of *Chrysopa rufilabris* lived for eighty-one days and a male of *C. quadripunctata* for fifty-nine days. The periods given in the preceding paragraph are the longest records for females of *C. oculata,* while the longest record for a male was thirty days. Adults of this species usually lived for two or three weeks in rearings, but the less common species, as *C. harrisii, C. lineaticornis, Allochrysa virginica,* and the species of Meleoma, could not be kept alive longer than a week, or at most ten days. Adults of *Chrysopa plorabunda* have been kept alive from October to April, but during the summer have not remained alive for more than three weeks.

NUMBER OF GENERATIONS IN A YEAR

The number of generations varies with the different species and with the latitude. A pair of the species *Chrysopa oculata* emerged in the laboratory on February 18, 1915, and by July 1 four generations had been reared. From fragmentary outdoor rearings and collections, there are apparently three generations of *C. oculata* in New York and four in Virginia. There are very likely four generations of *C. plorabunda* in Kansas, but only two of *C. cockerelli.* There are two generations of *C. lineaticornis* in Virginia, but collections would indicate only one of *Allochrysa virginica.*

HIBERNATION

The majority of the species of Chrysopidae winter as prepupae within their silken cocoons. It is usually stated that they winter as pupae, but by opening cocoons monthly during the winter, it was found that they remain prepupae. *Chrysopa plorabunda* normally overwinters as adults in Kansas. In the mild winter of 1920-21, this species was active almost all winter and could be taken in numbers on warm, sunshiny days. During the more severe winter of 1921-22, none could be found flying in the open nor caused to fly up by beating. *C. interrupta* was reported by Banks (1915) as hibernating at Mount Vernon. Adults of *C. vulgaris* have been reported by McLachlan (1869) as wintering in a hornet's nest. *C. flava* has been reported by several writers as wintering in the adult stage.

One species, *C. cockerelli*, was found to winter as practically grown larvae. Larvae of this species were kept alive over winter without food in an attic and in a cave. Furthermore, an overwintering larva was found on April 4, 1921, in an apple orchard under a piece of bark. In the South, Chrysopidae breed continuously through the year.

Repeated attempts to winter eggs, larvae, and adults of species other than those previously mentioned have failed. Adults of *C. rufilabris*, *C. quadripunctata*, and *C. harrisii* were kept alive until November and December in Virginia in outdoor protected cages, but they finally all died. Immature larvae of our common species die if they are not fed, and when they are fed they go on to maturity and spin cocoons in which they winter as prepupae.

During the winter cocoons of the tree-inhabiting species may be found in crevices of the bark on maples, oaks, and elms, on leaves in heaps along hedgerows, and in similar protected places according to the habits of the larvae.

Discoloration in hibernating adults

Overwintering adults are usually much reddened, and their green color is largely replaced by brown as a result of the cold and from lack of food. Banks (1915) reported discoloration in *Chrysopa plorabunda*. Kolbe (1893) stated that the green color of chrysopids was due to chlorophyll, and ascribed the color change of *C. vulgaris* in the fall and after death to factors causing a comparable change in the leaves in autumn.

Specimens of *C. rufilabris* taken at Milwaukee on September 27, 1918, soon after the first frosts, had an elaborate reddish color pattern over the entire body, and the wings were a decided brown. This discol-

oration was brought on gradually during the fall of 1918 in specimens of *C. rufilabris* and *C. quadripunctata* which were placed in outdoor cages and fed on a weak sugar solution. As the cold weather came on, the discoloration became gradually more pronounced. Discolored adults of *C. plorabunda* are very common in Kansas in the fall and spring. The reddening appears with the first cold weather in the fall and persists until the adults begin to take food in the spring. Some specimens retain a little of the green, but the majority lose most of the normal coloration. Both males and females overwinter and thus become discolored.

It has been found that at any time during the winter the discolored adults of *C. plorabunda* may be brought into the laboratory and the normal green color restored. It appears that food is more important than temperature in this restoration, though this species has not been observed to take any food in confinement other than water, weak sugar solution, plant sap, and, less commonly, crushed aphids. The coloration has been restored in from one to two weeks by feeding water alone, or sugar solution, while the insects were confined in the laboratory.

FIRST APPEARANCE OF THE ADULTS IN THE SPRING

The time of the first appearance in the spring varies with the manner of overwintering and the climate. Adults of *Chrysopa plorabunda* have been taken throughout the winter in Kansas. At Charlottesville, Virginia, the first adult of *C. oculata* was seen on March 20, 1919; at Ithaca the first adult was seen the first week in May, 1916, but it is doubtful whether this was among the first to emerge. Adults of *C. quadripunctata* and *C. nigricornis* were taken the latter part of May, 1921, in Kansas, and in June, 1917, at Ithaca and in Kansas. It has been observed for four years that June is the earliest date when a variety of Chrysopidae has been taken by collecting. Adults were obtained during all the winter and spring months by bringing overwintering cocoons indoors, into a room of fairly constant temperature. Some individuals pupated promptly, while others made apparently no change for a month or more. Some prepupae died when brought indoors in the course of these studies, but pupae very rarely died in cocoons.

FACTORS REDUCING THE NUMBER OF INDIVIDUALS

Several papers dealing with the parasites of the Chrysopidae have been published. Howard (1888), Girault (1907 b), and McGregor (1917) have given lists of parasites. Moffat (1901) discusses egg parasitism but lists no species. So far three egg parasites, one larval parasite,

sixteen primary pupal parasites, eight secondary pupal parasites, and one adult parasite, have been recorded for the Chrysopidae. The predacious enemies recorded are certain birds (Wildermuth, 1916), and a larva of *Anatis 15-punctata* (Schwartz, 1890).

Parasites

Egg parasites

Trichogramma minutum Riley was the only egg parasite reared during these studies. This parasite attacks the eggs of a large number of different insects, but, so far as is known, has not before been reported as attacking eggs of the Chrysopidae. Its life history has been given by Bodkin[3], together with valuable biological notes on the species. Parasitized eggs turned to a smoky color in about three days, and jet black with a peculiar dull appearance in another day. One egg was glued fast to a leaf by a gelatinous substance, but later examples show this to have been an exception. When mature the adult parasite emerged through an irregularly circular hole eaten in the side of the egg. This parasite is of no appreciable importance inasmuch as its occurrence in nature is rare. Its life history may be readily studied by obtaining the parasites from some other host—as, for example, eggs of the corn-ear worm *(Chlorida obsoleta* Fab.)—and inducing parasitism on chrysopid eggs.

Larval parasites

Only one parasite attacking the larva was taken. This was a parasitic chigger mite of the genus Erythraeus (Hartzel, 1918). While the writer was collecting on the grounds of the Soldiers' Home at Milwaukee on August 25, 1917, a number of larvae of *Chrysopa rufilabris* were taken which had one or more of these bright red mites attached. They remained attached to the larvae for several days when the larvae were confined in vials, and a few remained permanently attached when the larvae were preserved in alchohol. Larvae thus parasitized showed very slow growth.

Pupal parasites

Considering the word *pupa* here as including the prepupa, which stage is also spent inside the cocoon, a number of important pupal parasites have been obtained. The primary and secondary parasites that have emerged from cocoons are given in the accompanying table.

[3]Bodkin, G. The egg parasite of the small sugar cane borer. Board Agr. British Guiana. Journ. 6:188-198. 1903.

Parasite	Host species	Locality	Date	Determined by
Helorus chrysopae	*Chrysopa oculata* (?)	Ithaca	August 25, 1916	Dr. J. C. Bradley
Perilampus sp.	*C. oculata* (?)	Ithaca	August 22, 1916	Professor C. R. Crosby
Hemiteles areator subsp. *tenellus*	*C. nigricornis*	Ithaca	October 20, 1916	Dr. J. C. Bradley
Hemiteles tenellus Say	*C. rufilabris*	Charlottesville	August 11, 1918	A. B. Gahan
Perilampus chrysopae Cwfd.	*C. rufilabris*	Charlottesville	August 11, 1918	A. B. Gahan
Tetrastichus chrysopae Cwfd.	*C. rufilabris* (secondary)	Charlottesville	August 11, 1918	A. B. Gahan
Arachnophaga sp.	*C. lateralis*	Florida	September 4, 1918	A. B. Gahan
Parataneostigma nigriaxillae Gir.	*C. lateralis*	Florida	September 9, 1918	A. B. Gahan
Isodromus atriventris Ash.	*C. lateralis*	Florida	August 24, 1918	A. B. Gahan
Horismenus sp.	*C. lateralis*	Florida	September 12, 1918	A. B. Gahan
Dibrachys bouchearus Ratz	*C. rufilabris* (secondary)	Milwaukee	August 25, 1917	A. B. Gahan
Perilampus chrysopae Cwfd.	*C. rufilabris*	Dayton, Ohio	August 26, 1921	A. B. Gahan
Tetrastichus (Geniocerus) chrysopae Cwfd.	*C. rufilabris*	Dayton, Ohio	August 26, 1921	A. B. Gahan

The information obtained concerning the life histories of these parasites and hyperparasites is fragmentary. Parasitized cocoons in all cases gradually turn dark to decidedly black. When parasites have emerged, one can usually find the shriveled skin of the prepupa in the

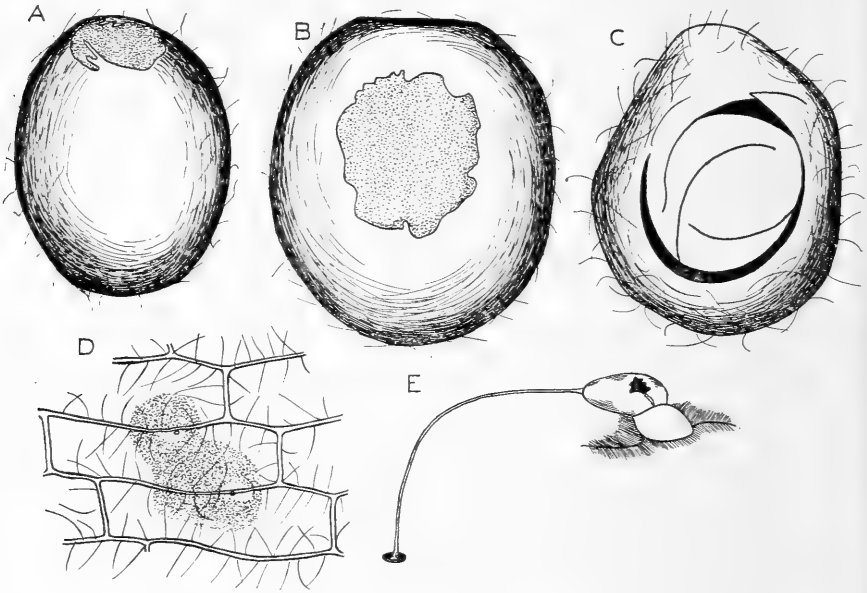


FIG. 160. WORK OF PARASITES ON CHRYSOPIDS

A, Empty cocoon of Chrysopa rufilabris from which Hemiteles areator subsp. tenellus emerged, x 11¾
B, Cocoon of C. oculata from which Perilampus sp. emerged, x 11¾
C, Cocoon of C. oculata from which Helorus chrysopae emerged, x 11¾
D, A piece of a wing of C. oculata showing two feeding punctures of Pseudoculicoides eques and the brownish area around each
E, Egg of C. oculata from which Trichogramma minutum emerged, showing the clear gelatinous substance holding the egg to the leaf, x 11¾

case, together with the thin, filmy cocoon of the parasite. In all cases so far seen, the parasite destroys the chrysopid prepupa before it pupates. The parasites make several kinds of openings in the cocoons at emergence, that of *Helorus chrysopae* being especially interesting (fig. 160, C).

In general, the pupal parasites are the greatest check on the Chrysopidae. Parasitized cocoons of *Chrysopa rufilabris*, *C. nigricornis*, and others occurring in the open, were frequently collected. McGregor

(1914), and McGregor and McDonough (1917), reported a parasitism of 55.9 per cent. There was never a parasitism even approaching this figure noted during these observations.

Parasites of the adult

Pseudoculicoides equus Johannsen (Plate LXXXVIII) was found to be fairly common on the wings of several species of Chrysopidae. This is a little blood-sucking chironomid, which sits on the wings, buries its proboscis in a vein, and sucks up the blood of its host. At Ithaca during the month of July, 1916, an average of 9.5 per cent of all the *Chrysopa oculata* adults collected had one or more of these parasites on their wings. They were taken on the wings of *C. oculata* and all its varieties, *C. chi* and its variety, *C. nigricornis,* and *Meleoma signoretti.* The parasites appear to have no choice as to the veins of their host, and as many as three may be found on one wing. They sit motionless while on the wings and hold on firmly even while the host is flying. The abdomen is generally distended. When disturbed the parasites fly very rapidly, practically leaping from place to place. Only females were found on the wings. The life history is unknown. The species was observed only in New York State.

The parasitic mite Erythraeus also attacks the adult chrysopids. The mite remains securely attached to the body of its host. Specimens of *C. rufilabris* thus parasitized were taken on goldenrod in the woods, at Milwaukee.

Predacious enemies

Wildermuth (1916) points out that certain birds, such as the western wood pewee and the nighthawk, feed on adult Chrysopas in spite of their repellent odor. He states also that robber flies have been noted as catching the adults, and that some Hemiptera prey on the larvae. The writer has given live adults to a praying mantis, which devoured several daily. A red-headed woodpecker was seen to catch an adult, probably *Chrysopa nigricornis,* on the wing and devour it. It was observed that coccinellid larvae would eat eggs of *C. oculata* but did not devour larvae of the same species.

FACTORS AFFECTING THE SPREAD OF THE SPECIES

Most of the species of Chrysopidae studied have a wide distribution. Their flight is not adapted to long distances. It seems probable that the gradually increasing range of the species is being brought about

through the shipping of hay, grass, logs, trees, shrubbery, and the like. Cocoons occur on various parts of these and may readily be shipped even to considerable distances. Professor C. R. Crosby found fourteen chrysopid eggs on the window of a moving train, and this suggests a ready means of spread. Adults may enter open box cars during the day and be transported to a considerable distance.

ECONOMIC IMPORTANCE OF THE FAMILY

Both larvae and adults of all our species of Chrysopidae are distinctly beneficial. The only instance on record of this family's doing any harm was in California, where the larvae were reported by Essig (1911) as destroying the larvae of ladybird beetles which had been introduced to combat scale insects. During the course of these rearings several species of coccinellid beetles were successfully reared in the same vials with chrysopids, but there were usually some aphids present.

Chrysopid larvae are occasionally an annoyance to man by their biting, which suggests a pin prick, and by their crawling over his person. This occurs most frequently under trees or in fairly dense vegetation. The tree and shrub chrysopid species are most commonly the source of this annoyance, but any hungry, grown, third-instar larva appears to be capable of piercing the skin and sucking some blood if not disturbed (Marchand, 1922).

The chief contribution of the Chrysopidae to human welfare is their destruction of plant lice during the summer and autumn months. They do not appear early enough in the year, nor are they present in sufficient numbers, to appreciably check fruit injury by plant lice or to reduce early spring outbreaks of aphids such as that of the pea aphids on alfalfa in Kansas early in 1921. But as summer progresses, the tree-inhabiting species become sufficiently numerous to take an important part in combating the woolly apple aphis on elm, the painted maple aphis, the maple Phenococcus, the apple leaf hopper, and similar pests. Aphids attacking cereal and forage crops are preyed upon by *Chrysopa oculata*, *C. plorabunda*, and *C. rufilabris*, chiefly. These species are usually present in clover and alfalfa fields, sorghum fields, and cornfields, sometimes in great numbers. While it is the larvae that are generally seen devouring the plant lice in the field, nevertheless there is no doubt that the adults of our common species regularly prey upon plant lice, with the possible exception of *C. plorabunda*, and thereby increase the importance of this family economically.

One is likely to give the Coccinellidae and the Syrphidae some of the credit for aphid destruction which is really due to the Chrysopidae,

for, on examination of an aphid-infested plant, these insects are usually first seen, the chrysopids being more difficult to find.

The parasitic Hymenoptera and the Coccinellidae are generally more plentiful and more effective checks upon aphids than the chrysopids, though this varies with the locality and other conditions. In one field where the melon aphis was plentiful, these enemies were very scarce while *Chrysopa oculata* was exceedingly abundant.

DESCRIPTIONS OF THE LIFE STAGES OF THE SPECIES

It will be soon observed that the chief points emphasized in the following descriptions are color patterns. The reader is cautioned against too strict interpretation of color shades and of sizes and shapes of spots, for both are subject to variation. However, the variation does not extend to such lengths as to make the species difficult to recognize, with the possible exception of the *rufilabris-plorabunda group*. With a little practice, all the larvae described may be recognized at a glance in the third instar. The other instars are more difficult of recognition because of size and less distinct coloration.

Chrysopa oculata Say (Plate LXXIX)

1839 *Chrysopa oculata.* Say, Journ. Acad. Nat. Sci. Phila., vol. 8, p. 9-46.
1839 *Chrysopa chlorophana.* Burmeister, Handbuch Ent., vol. 2, p. 979.
1855 *Chrysopa albicornis.* Fitch, First report, p. 84.
1903 *Chrysopa chlorophana.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 147.
1903 *Chrysopa albicornis.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 149.
1903 *Chrysopa oculata.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 152.

Chrysopa albicornis Fitch is placed under *C. oculata* Say for the following reasons:

1. There is no definite boundary between the two forms, the only differences being in their size and in the degree of darkening of the wings. A series may be readily arranged from one to the other.

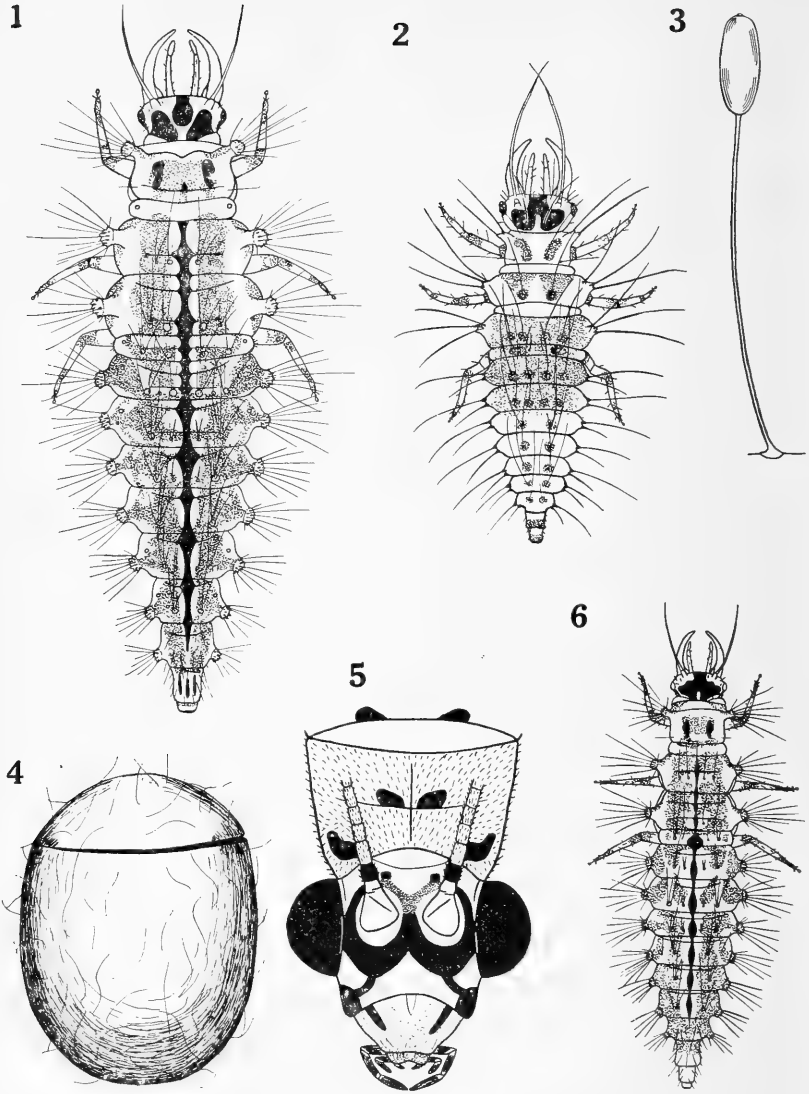
2. The great majority of specimens answering the description of the former are males. It has been found that the males show a tendency to be smaller and darker than the females.

3. The progeny of several females answering the description of *albicornis* gave all medium-dark-winged to light-winged specimens *(oculata).*

4. The dark specimens cross readily with any variety of *C. oculata.*

5. The dark specimens occur with *C. oculata* in nature in the same habitats and have no distinguishing habits.

6. The eggs and the larvae of the two forms are indistinguishable.



CHRYSOPA OCULATA

1, Mature third-instar larva, x about 10¾. 2, Newly hatched first-instar larva, x about 18; dotted part of abdomen showing coloration due to first meal. 3, Egg, x about 10¾. 4, Cocoon, showing lid, x about 10¾. 5, Head and prothorax of adult, showing color pattern, x about 10¾. 6, Second-instar larva, x about 10¾

C. chlorophana Burm. is included under *C. oculata* Say for the following reasons:

1. The progeny of wholly-green-winged females have nearly always been *oculata*. Very few forms with wings of a permanently pure green have yet been obtained in rearings from any variety of *oculata*.

2. The great majority of individuals of this variety have been found to be females. Males are scarce. Females of *C. oculata* of the dark medium type tend to be larger and have lighter wings, and so a series can be arranged from the darkest to the wholly-green-winged varieties.

3. *C. chlorophana* crosses readily with any variety of *C. oculata*, including *albicornis*.

4. It occurs in nature with *C. oculata* and can be taken in the same habitat.

5. The life history stages of the two forms are indistinguishable.

The average length of time for the various stages of the life history of ten individuals of *Chrysopa oculata* reared in the laboratory in the early spring of 1916 was, respectively: egg stage, 5.4 days; first instar, 7.3 days; second instar, 3.9 days; third instar to spinning of cocoon, 3.9 days; within the cocoon, 26 days.

This is by far our most abundant species. The writer has collected specimens in New York, Ohio, Virginia, Wisconsin, and Kansas. The species is a member of the field group, and in general collecting in the East it always predominates. It has the greatest range of any of our species. Descriptions of the stages from the medium-dark-type parentage only are here given, as the types are all identical.

Egg.—Elongate-elliptical, light bluish or yellowish in color, normally on a long, hyaline stalk. Chorion smooth, unmarked. Micropyle button-like, white, rarely with a tinge of green. Length of egg, 1.03 to 1.1 mm.; diameter, 0.42 to 0.49 mm.; length of stalk, 3.4 to 4.8 mm.

First-instar larva (just hatched).—A large black spot on dorsum of head, deeply notched behind. Body gray to flesh-colored. Two setae from prothoracic tubercles; three from each mesothoracic and metathoracic tubercle; two each, an upper large one and a lower small one, from abdominal tubercles 2 to 7; dorsal tubercles on thorax prominent, each bearing a single seta; an outer pair of dorsal tubercles and an inner pair of papillae on each of abdominal segments 1 to 6, each bearing a single seta. Dark spots around base of each of the abdominal dorsal papillae and tubercles. Total length of larva, 1.88 mm.; length of head, 0.54 mm.; length of mandibles, 0.39 mm.; width of head, 0.33 mm.; width at metathorax, 0.38 mm.; length of longest setae on body, 0.47 mm.

Second-instar larva.—Head with same coloration as in previous instar; antennae, jaws, and palpi yellowish to brownish in color; prothoracic tubercles prominent, dark in color; a patch of light brown or reddish brown on anterior side of stalk. About ten long and short setae from each tubercle. Mesothorax

and metathorax very similar; first subsegment of mesothorax entirely grayish, less commonly with slight reddish areas on each side of dorsal vessel; first subsegment of metathorax very small, entirely gray except a small white spot on each side of dorsal vessel; second subsegment of each of similar color pattern; tubercles entirely white to light grayish; on each side of dorsal vessel a white area. First segment of abdomen rounded at sides, not bearing tubercles; lateral tubercles on second segment prominent, dark brownish black; on segments 3 to 7 inclusive, lateral tubercles white, with a small, reddish brown, elongate spot on upper side of each stalk; setae and their bases black; outer dorsal tubercles bearing two setae each, the inner pair one each; just in front of outer pair of dorsal tubercles, a prominent reddish brown to flesh-colored spot. Total length from tail to tips of mandibles, 4.8 mm.; width at metathorax, 1.3 mm.; length of mandibles, 0.53 mm.; width of head, 0.6 mm.; length of head, 0.3 mm.

Third-instar larva.—General coloration and form very similar to that of second instar. Dorsal head pattern distinctive of instar. Head grayish, with three large, distinct, black spots on dorsum; mandibles amber-colored; antennae dark. Legs dark near joints. First subsegment of prothorax having grayish area in median line; base of first pair of tubercles reddish brown; second and third lateral tubercles yellowish, bearing fifteen to twenty setae each; a large reddish brown patch near base of stalk on anterior side of each; an irregular reddish brown area on each segment from base of stalks to yellow border of dorsal vessel. First pair of lateral abdominal tubercles lacking; second pair brownish black, specific; other tubercles reddish brown, but with their bases yellow, forming an irregular yellow border for the abdomen on each side; reddish brown area extending forward in front of each abdominal tubercle, reaching yellow border of vessel; a yellow area reaching this reddish area just in front of it. Eighth abdominal segment yellowish in center, borders pale; ninth segment with brown area in front; tenth segment nearly wholly brown. Length, 9 mm.; width at metathorax, 2 mm.

Pupa.—(The larva usually spins a pure white silken cocoon, but it may fail to do this.) Appearance of cocoon papery, with straggling threads issuing. Length of cocoon, 3.4 to 3.6 mm.; width, 2.7 to 2.9 mm. (For characters of pupa, see head characters of adult).

Adult.—Face pale yellowish; two broad loops of shining black under both antennae; median prong of color ending between antennae; a prominent loop of black near each eye, joining sub-antennal loops; a red or reddish yellow triangle above, with four occipital dots above this, these dots often connected; occiput distinctly yellow; basal joint of antennae and antennal areas of head gray to yellowish; second joint of antennae with black ring; remainder of antennae very light brown; clypeus reddish, with black dots at sides; labrum reddish; palpi broadly banded with black. Two prominent black spots at outer anterior margins of prothorax; eight small black dots on dorsum of prothorax behind these, often indistinct. Thorax and abdomen light green, generally unmarked except by darkened areas of viscera. Wings hyaline, varying from having all veins and veinlets green to a considerable degree of darkening; tips rounded. Length from head to tips of wings, 15 to 20 mm.

Chrysopa nigricornis Burmeister (Plate LXXX)

1839 *Chrysopa nigricornis.* Burmeister, Handbuch Ent., vol. 2, p. 979.
1861 *Chrysopa nigricornis.* Hagen, Synopsis Neuroptera N. Amer., p. 214.
1903 *Chrysopa nigricornis.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 149.

Chrysopa nigricornis is one of our largest species. Adults can be taken at lights from June to September. This is a tree and shrub species. Larvae have been repeatedly taken on maple trees in late summer, when the painted maple aphis is most abundant. The species has also been taken repeatedly on oak, elm, tulip tree, spiraea, and red osier (dogwood). Specimens have been collected at Ithaca, Milwaukee, Dayton, Charlottesville, and Manhattan (Kansas).

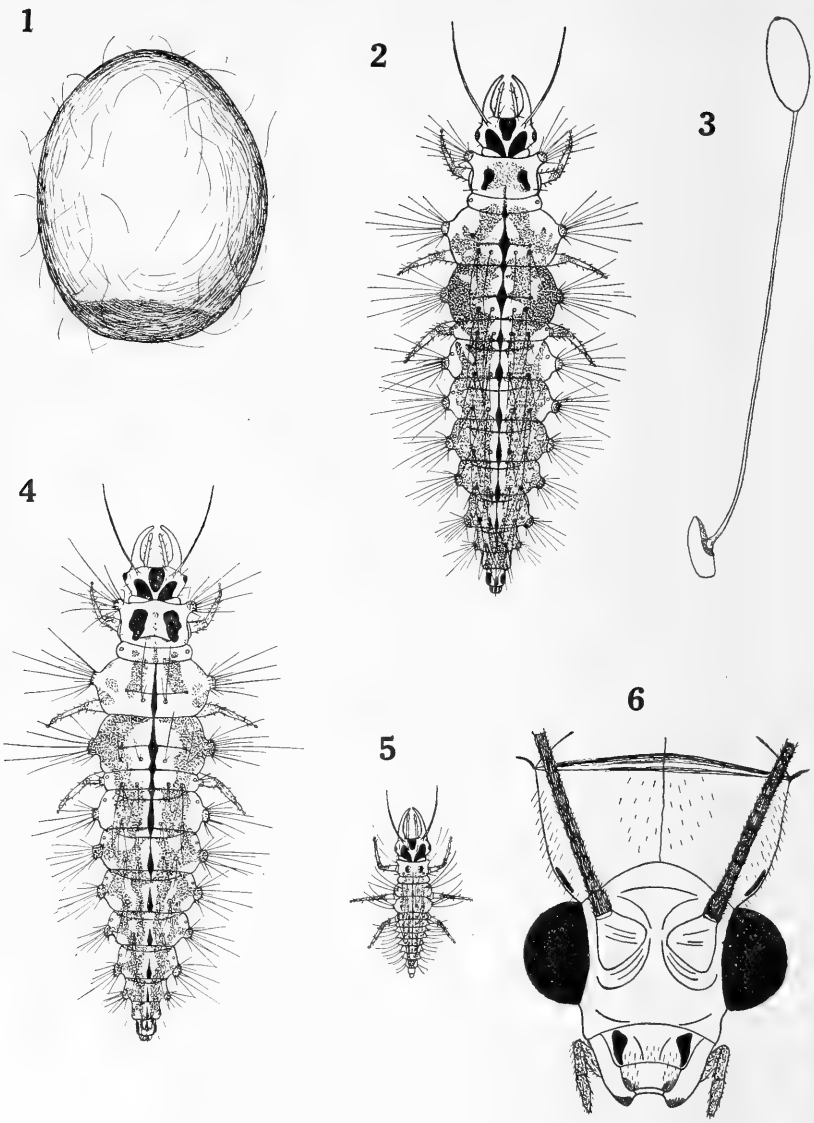
The life history of some of the specimens observed may be summarized as follows:

Number of specimen	Date egg was laid	Date of hatching	Date of first molt	Date of second molt	Date cocoon was spun	Date adult emerged
54.1	Sept. 2	Sept. 7	Sept. 11	Sept. 16	Sept. 28	Wintered
54.3	Sept. 2	Sept. 7	Sept. 11	Sept. 17	Sept. 28	Wintered
54.2	May 22	May 27	June 6	June 9	June 12	June 25
56.4	Dec. 9	Dec. 16	Dec. 21	Dec. 24	Dec. 29	Jan. 9
67.5	May 22	May 28	June 6	June 9	June 12	June 28

Egg.—Elongate elliptical, light green with yellowish tinge, becoming more yellow as embryo develops. Eggs laid singly or in close groups. Length of egg, 1.02 to 1.09 mm.; width at middle, 0.38 to 0.42 mm.; length of stalk, 7.5 to 8.6 mm.

First-instar larva.—Head grayish or yellowish, large with three spots above. Thorax grayish to dark; whitish area on each side of dorsal blood vessel throughout its length. Two setae from prothoracic and all lateral abdominal tubercles; three setae each from meso- and metathoracic lateral tubercles. First two pairs of thoracic tubercles grayish to yellowish; third pair black or reddish; first pairs of lateral abdominal tubercles white, fairly well developed. Medial setae prominent. A dark spot at base of each dorsal abdominal tubercle. Length of newly hatched larva, 1.5 mm.; width of head, 0.32 mm.; width at metathorax, 0.32 mm.; length of lateral setae, 0.29 mm.

Second-instar larva.—Three separate spots on dorsum of head. First two pairs of lateral tubercles grayish; third pair dark brown to blackish brown. First abdominal segment bearing a pair of small lateral tubercles beset with about five short, white setae. Dorsum of abdomen dark; border of gray on each side of vessel; near end of instar, reddish spots appearing in this gray border. First two abdominal tubercles white to gray; others dark to brownish black; tubercles bearing six to ten setae each, two large, the remainder smaller. Early second-instar larvae rather dark; late second-instar larvae reddish brown, much like *C. oculata*; color pattern tending to break up into irregular reddish brown patches. Legs wholly gray; distal ends of tibiae and tarsi black. Width of head, 0.57 mm.; length of mandibles, 0.49 mm.; length of antennae, 0.8 mm.; total length of larva, 5.95 mm.; length of setae, 0.46 mm.



CHRYSOPA NIGRICORNIS

1, Cocoon, showing black disk of last larval molt. 2, Mature second-instar larva. 3, Normal egg. 4, Early third-instar larva. 5, First-instar larva, just hatched. 6, Head of adult, the two-spotted type

(All x about 10¾)

Third-instar larva.—Head gray or yellowish; three separate black spots above; mandibles, palpi, and antennae light amber, tips of mandibles darker. First subsegment of thorax gray, darker at sides; second subsegment largely dark brown to brownish black, border smoky gray, reddish below; reddish between prothoracic depressions. First subsegment of mesothorax gray, crossed by reddish areas; second subsegment reddish black except grayish borders and a small gray area on each side of dorsal vessel; in these gray areas some bright red spots. Prothoracic and mesothoracic tubercles similar, bearing twelve to eighteen setae; bases of all black; apical setae larger than basal ones. Metathorax black or brownish black except a prominent gray area on each side of vessel, with bright red spots in same. First abdominal tubercle well developed, pure white, bearing white setae; second pair of tubercles also white, with a tinge of red on stalks; remainder of tubercles alike, grayish variously marked with dark red, bearing twelve to fifteen setae, three to five large black ones and the remainder smaller and white; from border to gray area along vessel, black, almost uninterrupted in early third-instar larvae, later breaking up into poorly defined reddish black blotches. Width of head, 0.92 mm.; length of mandibles, 0.8 mm.; total length of larva, 9.1 mm.; width at metathorax, 3 mm.; length of abdominal setae, 0.7 mm.

Pupa.—Pupal stage generally passed in a silken cocoon. Cocoon elongate spherical, pure white, appearing like paper but with few free threads; opening by lid at upper end. Length of cocoon, 4.1 mm.; width, 3.3 mm. (For late pupae, the head characters of the adult are useful in identification.)

Adult.—Head grayish green, darker above; usually two elongate marks on outer margins of clypeus (in some cases two more black dots on genae); clypeus with row of setae; labrum distinct, bordered with setae; area about basal antennal joint depressed, first joint grayish green, from the second to the end of about the basal fifth jet black to brownish, fading into light brown which persists to tip. Prothorax wholly green, usually with two black spots at outer anterior margins; two or three small median black dots seen in some specimens, otherwise entire thorax and abdomen light green. Wings long, acute at tips, rather narrow; pterostigma prominent; gradate veinlets and others dark. Length of adult, 15 to 20 mm.

Chrysopa quadripunctata Burmeister (Plate LXXXI)

1839 *Chrysopa quadripunctata.* Burmeister, Handbuch Ent., vol. 2, p. 980.
1851 *Chrysopa quadripunctata.* Schneider, Symb. ad monograph. gen. Chrysopae, p. 84.
1861 *Chrysopa quadripunctata.* Hagen, Synopsis Neuroptera N. Amer., p. 218.
1903 *Chrysopa quadripunctata.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 153.

The species *Chrysopa quadripunctata* also is arboreal. It was taken most frequently in a dense thicket of oak and underbrush at Charlottesville; at lights and by sweeping goldenrod in shaded localities, preferably near oaks and on maple and spiraea, with *C. nigricornis*, at Ithaca and Milwaukee; in dense woods on goldenrod at Dayton; on elm, maple, and apple at Manhattan. This is a very beautiful species and is quite distinct. In habits it is much like *C. nigricornis*, except that the larvae are very frequently seen with some trash on their backs.

The life history as observed in some specimens may be summarized as follows:

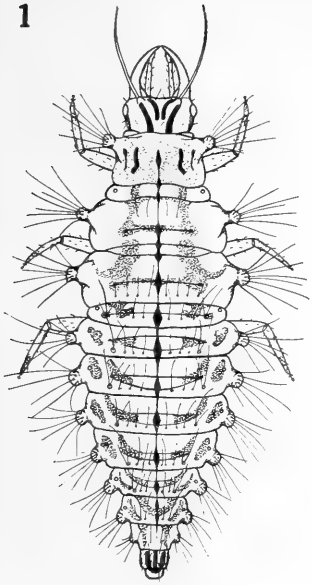
Number of specimen	Date egg was laid	Date of hatching	Date of first molt	Date of second molt	Date cocoon was spun	Date adult emerged
71	Sept. 9	Sept. 15	Sept. 19	Sept. 24	Oct. 8	Wintered
72	Sept. 7	Sept. 11	Sept. 15	Sept. 20	Sept. 28	Wintered
73	Sept. 6	Sept. 10	Sept. 14	Sept. 18	Oct. 3	Wintered

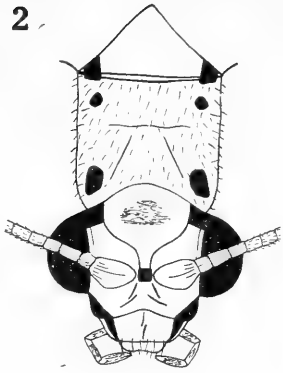
Egg.—Stalked, laid singly; oftenest found on trees (especially maple) and shrubs. Smaller than most chrysopid eggs, very light green to yellowish green. Chorion unsculptured. Length of eggs, 0.84 mm.; width, 0.38 mm.; length of stalk, 4.4 to 4.6 mm.

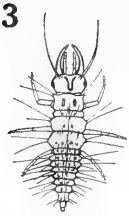
First-instar larva.—Very pale, somewhat translucent. Contractions of pharynx observable as larva feeds, appearing as an hourglass-shaped structure in dorsal view, slightly darkened; later four narrow bands on dorsum of head, converging behind. Body unmarked except anterior of abdomen, which is darker, due to food. Lateral tubercles prominent; setae long and stout, two on each prothoracic tubercle, three on each meso- and metathoracic lateral tubercle. No setae on first abdominal segment, which is also without tubercles; on each of lateral tubercles 2 to 7 inclusive, two setae, a large upper and a small lower one; two pairs of dorsal papillae on each abdominal segment from first to sixth inclusive; on thorax and beyond sixth segment, but one pair each.

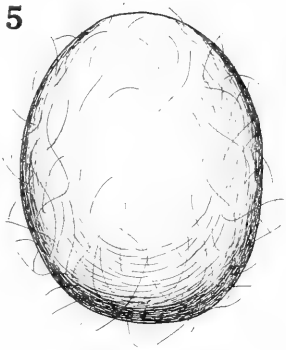
Second-instar larva.—General color gray, with brown to brownish black markings. Head entirely gray above; two pairs of converging black marks at midline; two narrow bands extending posteriorly from outer margin of antennae and converging; two others between these, shorter, converging behind. First subsegment of prothorax grayish white, both above and on sides. Thoracic tubercles large and prominent, wholly light grayish in color; setae medium long, eight to ten on each tubercle; paired dark brownish to black markings on thorax at each suture; black of dorsal vessel widening out at each suture, between these large patches of color and the sides, smaller areas of reddish brown. Fifth, sixth, and seventh abdominal segments with a little of this reddish brown mixed in the large spots; eighth abdominal segment with a large central black spot; ninth with a basal black spot; tenth slightly yellowish brown, without dark spots; segments 2, 3, 4, and 5 showing brownish spots on sides beneath lateral tubercles; a few dorsal setae, small and inconspicuous, most prominent on segments 5, 6, 7, and 8.

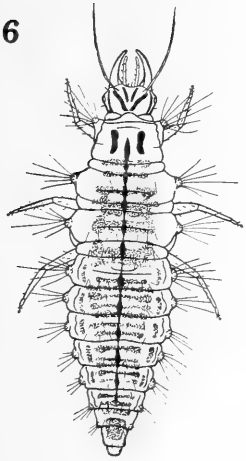
Third-instar larva.—General color gray, marked with brown to brownish black. Head grayish, four converging narrow brown bands above; middle pair of bands short, curved toward each other abruptly, and extending posteriorly to middle of head; outer pair narrow in front, broadening out in posterior half, extending from bases of antennae to first subsegment. Lateral tubercles of thorax and abdomen wholly gray. Two patches of brownish extending from prothoracic depression to metathorax, these increasing in width until they are broadest at metathorax, so that this is the darkest part of the body. Prominent gray bordering each side of dorsal vessel. Thoracic markings extending back over abdomen to fourth abdominal segment, decreasing in intensity and disappearing at fourth segment; from fourth to seventh segment, abdomen mostly

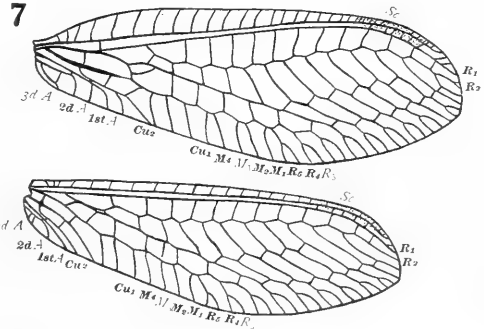












CHRYSOPA QUADRIPUNCTATA

1, Third-instar larva, about midway in the instar. 2, Head and prothorax of adult, showing markings. 3, Newly hatched larva. 4, Normal egg. 5, Cocoon. 6, Second-instar larva. 7, Right wings of adult
(All x about 10¾)

gray; first abdominal segment with no prominent lateral tubercles but some short setae on sides; some variation in coloration, chiefly in the amount of brown. (This larva was nearly ready to pupate; less advanced ones are darker.)

Pupa.—Cocoon slightly elongate spherical, of dense, pure white silk. Length of cocoon, 3.4 mm.; width, 2.6 mm. Late pupa with markings of adult faintly outlined. Early pupae difficult to classify.

Adult.—Head yellow above, gray below; antennae with a prominent reddish brown or maroon stripe from eyes to mouth; an orange spot between bases of antennae; a pair of elongate orange spots above eye; occiput pure yellow; distal segment of palpi brownish; antennae wholly pale. Body bluish green, with a fairly prominent yellowish dorsal area. Prothorax marked above with two pairs of orange spots. Mesothorax with a pair of orange spots in front. Abdomen yellowish above, green on sides; first three segments variously marked with orange on sides. Wings fairly broad; front pair scarcely acute at tips; hind pair acute at tips; gradate veinlets brownish black; ends of costals and radial sectors brown; pterostigma distinct. Length of adult, 12 to 16 mm.

(There is some variation in the size and intensity of the color spots. The orange spots vary to reddish and the yellow dorsal area varies in prominence. There is also some variation in the length of the adults.)

Chrysopa chi Fitch (Plate LXXXII)

1855 *Chrysopa chi.* Fitch, First report, p. 87.
1855 *Chrysopa upsilon.* Fitch, First report, p. 87.
1861 *Chrysopa chi.* Hagen, Synopsis Neuroptera N. Amer., p. 213.
1861 *Chrysopa ypsilon.* Hagen, Synopsis Neuroptera N. Amer., p. 213.
1903 *Chrysopa chi.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 148.
1903 *Chrysopa ypsilon.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 148.

The two species *Chrysopa chi* and *C. upsilon* are described by Fitch and designated the *X* and *Y spotted golden eyes.* Hagen (1861) redescribed both species, and after his description of *C. "ypsilon"* he added: "At first sight it resembles the preceding [*C. chi*]; is it different?" Banks (1903) describes the two species in comparison, and adds: "It [*C. "ypsilon"*] is very close to *Ch. chi,* but the difference in head-markings appears to be constant."

The writer has carefully reared both the *X* and the *Y* variety, and has concluded that they are the same species for the following reasons:

1. Batches of eggs from either variety yielded adults marked the same as the other, as well as intermediate varieties.

2. The larval colorations were identical.

3. The adults of both varieties occurred in the same habitats.

4. There was an intergradation of the head markings. Six steps in this intergradation are shown in Plate LXXXII, 7, and others may be added though they are less distinctive. To illustrate the proportion of each of these steps, the catch from a trip on June 22, 1916, was classified. These specimens were all taken within an area of an acre. Of the 87

specimens, 20 were No. 1, or true *C. chi,* 17 were of the second variety, 10 were of the third, 15 were of the fourth, 11 were of the fifth, and 14 were of the sixth, or true *upsilon,* variety.

Both of these species were described by Fitch at the same time, and on the same page of his report. *C. chi* was the first described, and therefore becomes the true species, and *C. upsilon* becomes a synonym. It appears from rearings and collections that *C. chi* is slightly more abundant than *C. upsilon.* It is an early species, having been found fairly abundant at the McLean bogs in the middle of June, in goldenrod patches. It has been taken also in Ithaca, along shaded hedges and on spiraea, in June.

The life history of some specimens of *C. chi* may be summarized as follows:

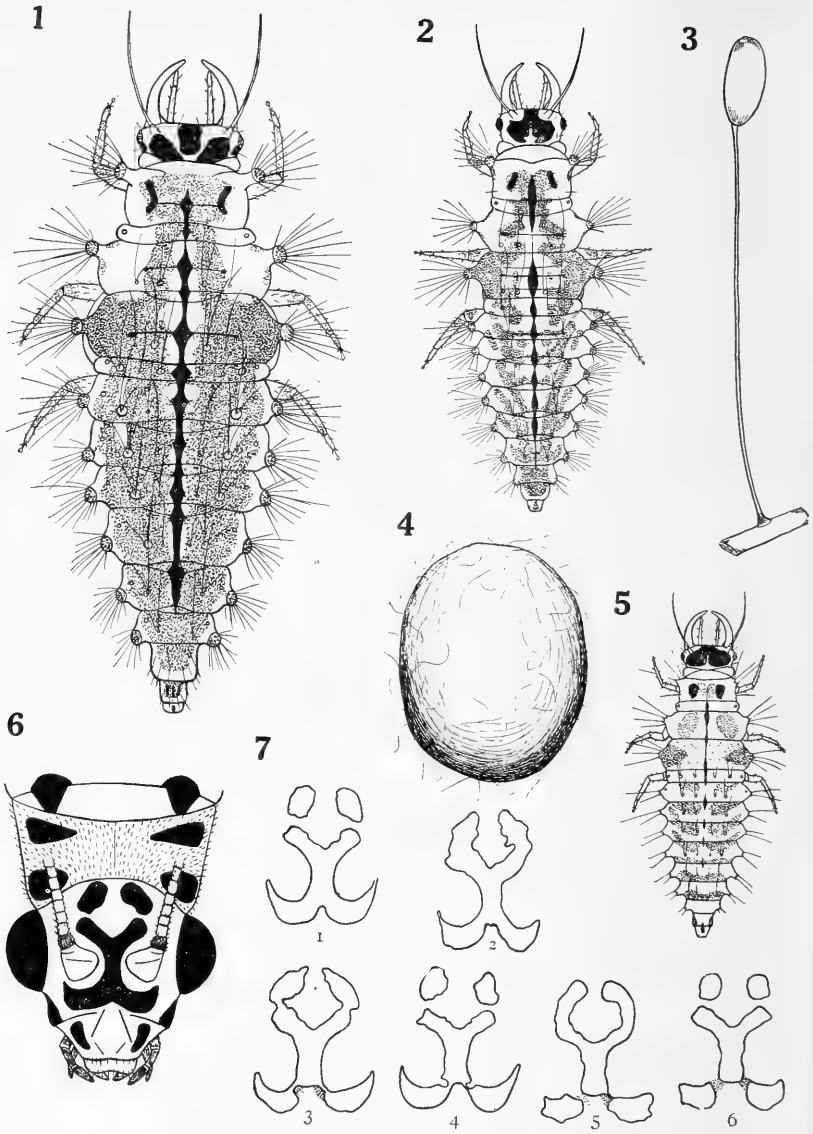
Number of specimen	Date egg was laid	Date of hatching	Date of first molt	Date of second molt	Date cocoon was spun
57.1	July 15	July 20	July 23	July 26	Aug. 2
57.2	July 15	July 20	July 23	July 26	July 30
57.3	July 15	July 20	July 24	July 26	Aug. 1

The life history of some specimens of the *upsilon* variety was as follows:

Number of specimen	Date egg was laid	Date of hatching	Date of first molt	Date of second molt	Date cocoon was spun	Date adult emerged
60.1	July 15	July 20	July 24	July 27	Aug. 1	Aug. 15
60.2	July 15	July 20	July 24	July 26	July 30	Aug. 15
60.3	July 15	July 20	July 24	July 25	Aug. 1	Aug. 15

Egg.—Light bluish green in color, with a distinct yellowish tinge. Normally stalked, laid singly. Micropyle white; micropylar network pattern indistinct. Length of egg, 0.99 to 1.07 mm., average 1.05 mm.; diameter, 0.46 to 0.5 mm., average 0.49 mm.; length of stalk, 4.49 to 5 mm., average 4.68 mm.

First-instar larva (one day old).—Almost identical with the first-instar larva of *C. oculata.* One large black spot covering dorsum of head; a prominent notch at posterior border, extending nearly to middle. All lateral tubercles except meso- and metathoracic having two prominent setae projecting laterad; meso- and metathoracic lateral tubercles having three setae each; lateral tubercles fairly prominent. Body entirely yellowish gray; a pair of brownish spots in front of mesothoracic depressions; metathoracic tubercles with a large area of basal part brownish, this being the darkest part of the body. First abdominal segment without lateral tubercles; segments 5 to 8 inclusive with brown spots at base of large outer pair of dorsal tubercles; tenth segment with three longitudinal dark lines; dorsal tubercles on segments



CHRYSOPA CHI

1, Mature third-instar larva. 2, Second-instar larva. 3, Normal egg. 4, Cocoon enclosing pupa. 5, First-instar larva. 6, Head and prothorax of adult showing markings. 7, Series from specimens of inter-antennal markings to show gradation from X to Y; 7_1, a typical X, or C. chi; 7_2, the sub- and supra-antennal dots are fused with the inter-antennal mark; 7_3, the separation of these dots has begun; 7_4, the supra-antennal dots have separated and the sub-antennal dots have retained only a small connection; 7_5, the sub-antennal dots have become disconnected; 7_6, a typical Y, or upsilon, variety

(All x about 10¾)

1 to 7 bearing two setae each; dorsal papillae very inconspicuous and having one small seta each. Total length of larva, extended, 2.04 mm.; width at metathorax, 0.76 mm.; width of head, 0.42 mm.

Second-instar larva.—General color gray, with reddish brown or brownish black markings. Head gray, with large, black, undivided patch above. First two lateral thoracic tubercles gray. Prothorax with large, brownish black, dorsal area between depressions. Anterior subsegment of mesothorax gray, crossed by reddish bands; posterior subsegment largely gray, but marked with red; stalks of tubercles white, but with traces of brown in front and behind. Metathoracic tubercles entirely brownish black to velvety black. Basal areas to whitish border of dorsal vessel of each stalk, the same in color, this being the darkest part of the body. First abdominal segment without definite lateral tubercles, but generally with a rounded swelling on each side; these swellings and the tubercles on segments 2 to 4 inclusive, gray; remaining tubercles also gray, but in some cases slightly marked with brown; eighth abdominal segment reddish yellow, with three black lines; ninth and tenth segments pale reddish yellow; lateral setae long, gray in color, six to fourteen from each tubercle; all thoracic papillae and dorsal abdominal tubercles and papillae to fifth segment, gray; on segments 5 to 8, dorsal tubercles black; abdomen with large, triangular, black color patches. All lateral tubercles gray except metathoracic. Total length from tips of jaws to tail, 0.29 mm.; width at metathorax, 1.42 mm.; width of head, 0.64 mm.; length of head and jaws, 0.96 mm.; length of longest thoracic setae, 0.76 mm.

Third-instar larva.—Color dark brownish red, with grayish or yellowish white border. Head with three large black spots above; antennae dark; jaws amber-colored. First subsegment gray. Between prothoracic depressions dark reddish. First two pairs of thoracic tubercles largely white; metathoracic pair dark reddish velvety brown; bases of stalks same color, causing this to be the darkest part of body; an irregular grayish or yellowish area on each side of dorsal vessel on thorax. Abdomen entirely reddish black except dorsal papillae and tubercles, which are yellowish. No lateral tubercles on first abdominal segment. Lateral tubercles back to eighth segment gray or yellowish; a dash of gray extending antero-laterad from each dorsal tubercle, this bar of gray, with the gray along the dorsal vessel and the light borders, being the only light areas on the abdomen. Stalks and bases of lateral tubercles gray or yellowish, forming a light border on each side of the abdomen; irregular paired yellowish marks on highest parts between sutures; setae long, prominent, from twelve to fifteen on each knob; ventral side of abdomen gray; from seventh segment caudad brownish, a pair of triangular brown patches from thorax to seventh segment. Width of head, 0.92 mm.; length of mandibles, 0.88 mm.; width at metathorax, 1.72 mm.; total length of larva, 7.1 mm.; length of longest setae, 1.2 mm.

Pupa.—Cocoon normally elongate spherical, of white, closely woven silk, of the texture of coarse paper; original framework giving it a slightly woolly appearance. Length of cocoon, 3.26 mm.; width, 2.71 mm. (For characters of pupa, see facial and prothoracic characters of adult.)

Adult.—Entire body largely light green in color. Head and thorax prominently marked with jet black; conspicuous Y-shaped mark between antennae; a pair of black spots below bases of antennae, and another pair above. (The inter-antennal spot may be variously connected with these spots, giving a variety of patterns. Frequently the connection is slight.) A large black spot

below each eye, and two small spots near the upper border of each eye; two black spots on outer borders of clypeus; labrum and mouth parts brownish; last segment of palpi banded with black, other segments spotted. Basal segment of antenna green, second segment with a black ring; remainder of antenna brownish. Three pairs of large black spots on pronotum, symmetrically arranged. Mesonotum also with three pairs of black spots, one behind the wings. Wings of moderate length, somewhat acute at tips, hyaline; longitudinal veins green; costal and radial cross-veins mostly blackened at one or both ends; gradate series wholly black; branches of radius black at base; wings as a whole dark. Length of adult, 13 to 16 mm.

(As previously pointed out, a series of six or eight varieties in the interantennal marks exists, but there appears now to be small necessity for their formal designation. Furthermore, there is a marked difference in the coloration of the venter of the abdomen. This is variously marked, from the commoner green to entirely brownish black.)

Chrysopa rufilabris Burmeister (Plate LXXXIII)

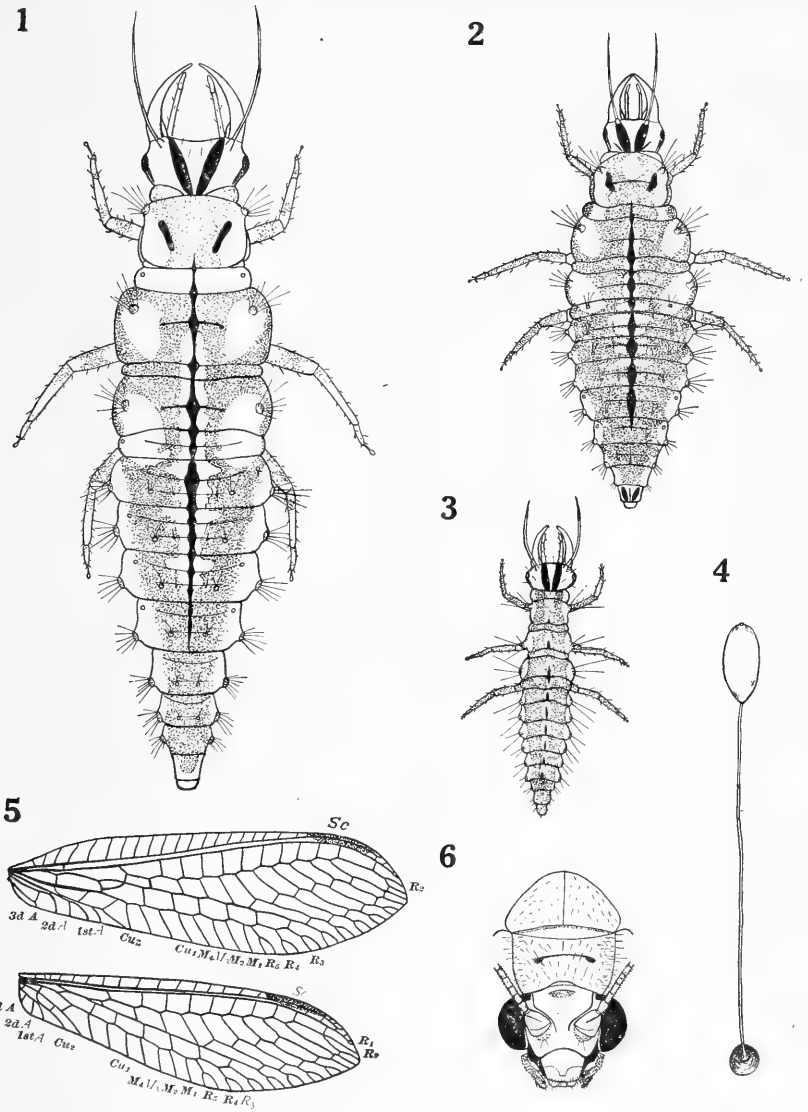
1839 *Chrysopa rufilabris.* Burmeister, Handbuch Ent., vol. 2, p. 979.
1851 *Chrysopa rufilabris.* Schneider, Symb. ad monograph. gen. Chrysopae, p. 79.
1861 *Chrysopa rufilabris.* Hagen Synopsis Neuroptera N. Amer., p. 219.
1903 *Chrysopa rufilabris.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 152.

The species *Chrysopa rufilabris* varies considerably and many specimens do not exactly fit descriptions. There appears to be a gradation from *rufilabris* to *interrupta.* In these studies the specific name *interrupta* was applied to very light, "straw yellow" specimens, and *rufilabris* to the darker forms. The latter are by far the most abundant. It is not unlikely that these two species are in reality one, but the writer has not had sufficient material of *interrupta* for study to justify definite conclusions.

C. rufilabris is widespread in its distribution. At Milwaukee, it was the most abundant species at lights. Specimens have been taken at Ithaca at lights, in woods, and in shaded goldenrod patches. At Charlottesville they were most abundant in a dense grove of oak and pine. At Dayton, Ohio, they were taken in a goldenrod patch along a fence in an *oculata* habitat. The species is predominately, however, a woods species.

Egg.—Elongate elliptical, very light green to faint yellowish green in color. Stalked, laid singly on leaves of maple and fruit trees, on grape, and on both trunk and leaves of oak. Length of egg, 0.88 mm.; greatest diameter, 0.48 mm.; length of stalk, 4.0 mm.

First-instar larva.—Head very large, out of proportion to remainder of body; gray, with two broad, longitudinal, convergent, faded black bands on dorsum, arising inside of bases of antennae, and extending posteriorly the entire length of head. Antennae and palpi grayish translucent. First subsegment of prothorax translucent; second subsegment wholly translucent but with pinkish tinge; depressions prominent, dark brown to black. Next two thoracic segments



CHRYSOPA RUFILABRIS

1, Mature third-instar larva, showing color pattern. 2, Mature second-instar larva a few hours before molting. 3, First-instar larva, about midway in the instar. 4, Egg. 5, Wings of adult, x about 3¼. 6, Head and prothorax of adult, showing coloration

(All except No. 5 x about 10¾)

and first eight segments of abdomen having same general pattern; each bearing a pair of prominent lateral gray tubercles and a pair of gray dorso-median tubercles with black tips; ninth segment of abdomen without lateral tubercles; tenth segment cylindrical, dark brownish black; each lateral tubercle bearing two setae except meso- and metathoracic pairs, which bear three each. Dorsal vessel indistinct; general color of dorsum faint pinkish, darker in anterior abdominal region due to food taken in. Legs translucent, with dark smoky areas on distal ends of femora and proximal halves of tibiae; tips of tarsi black. Length of larva, 1.2 mm.; width of head, 0.4 mm.; width at metathorax, 0.36 mm.

Second-instar larva.—Head with two large converging black spots above; jaws dark, tips amber; palpi and jaws with amber tinge. Prothorax with a light yellowish central area, on each side of which is a border of dark reddish brown. All tubercles very small, inconspicuous, white or light yellowish in color; stalks short; setae short. Between prothoracic depressions and extending posteriorly, a dark reddish brown area. Meso- and metathoracic tubercles having prominent yellow areas circling their bases, extending medianly and slightly posteriorly. On each side of the dorsal blood vessel a rather regular pinkish area. Abdomen bordered on each side by a white to yellowish white border, which increases in width to sixth segment; ninth segment with three dark spots above; tenth segment yellowish white. Between yellow side borders of abdomen and yellowish borders of dorsal blood vessel, color dark reddish brown. Legs very dark, blackened near joints.

Third-instar larva.—Head pale yellowish gray, with two longitudinal, jet-black, converging bars on dorsum, these bars pointed anteriorly and broadest at about the middle. First subsegment of prothorax smoky gray in color, crossed by two brick-red dorso-median bands which extend back over second subsegment and converge between its depressions; lateral tubercles and border of segment distinctly yellow. Mesothorax much like prothorax; entire median part a rich, velvety, very dark red; lateral tubercles prominent, wholly yellow, bearing from ten to fifteen colorless setae; a large yellow spot around base of each tubercle, giving segment a prominent yellow border on each side. Metathorax like mesothorax except that the posterior half of the median area is bright reddish while the anterior half is dark velvety red. Abdominal segments all of same general pattern, dorso-median part bright red, darker red outside this area, and yellow border, including lateral tubercles; eight to ten colorless setae from each lateral tubercle, and one or two small setae from two pairs of dorsal papillae on posterior third of each segment; posterior five or six segments darker red than anterior four or five; last segment largely black. Dorsal vessel dark red to black; border very light red, gradually increasing in intensity to dark red of dorso-median part. Venter gray; tubercles yellowish. Length of larva, 7.1 mm.; width at metathorax, 2 mm.

(There is a great variation in the intensity of the reds and yellows of this species in the same locality and in different localities, making this the most puzzling species yet studied. Some larvae are very light and faded, especially near the end of the third instar. In such cases they may show no trace of yellow in the borders, this color being replaced by some shade of gray. In some specimens the head spots extend in a gentle curve, in others they are distinctly angular. The writer has reared some twenty specimens of a species thought to be *C. harrisii*, but the emerging adults were as near *rufilabris* as *harrisii*. These larvae differed from *rufilabris* in having the jaws and the legs quite black, abdominal tubercles 2 to 4 inclusive marked slightly with reddish, and the general body color in some a duller red, and in others, or in different

stages within the instar, a purplish red. The adults had the characters of *harrisii* except that the gradates and a few other veins were partly marked with brown, the wings were less acute than in *harrisii*, and the head coloration was not quite true to description. Knowing the possibility of variations in this species, the writer hesitates to describe it as a new species until further rearing has been done.)

Pupa.—Cocoon silken, oblong spherical, white, closely woven but revealing the pupa within to a greater extent than in any other species seen; outer layer of cocoon fairly coarse, inner layer paper-like. Found commonly on maple leaves. Length of cocoon, 3.26 mm.; width, 3.07 mm. Pupa possessing facial characters of adult; body very light green in color. Total length of pupa, 4.03 mm.; width of abdomen, 7 mm.; length of wing pads, 1.92 mm.

Adult.—Very pale green to yellowish green, with ivory median stripe. Face yellowish white; a faded red stripe from each eye to mouth. Mouth parts and palpi yellowish. Basal joint of antenna yellowish gray, remainder of antenna light brownish. Legs yellowish gray, with a tinge of green in parts. Under side of body yellowish. Wings long, very slender; apex angular; gradate veinlets light brown, costal veinlets brown at ends, many others wholly or in part light brown; longitudinal veins all very light green; veins of hind wings all very light green except gradates and costals. Total length of adult, 14 to 16 mm.

(There is considerable variation in the adult, especially in color shades. The shape of the wings appears to be constant, likewise the brown color of the gradates. The body appears to vary in color from distinctly green to almost gray. The median dorsal stripe varies from yellowish to ivory white. The red stripe from the eyes to the mouth varies from distinct cherry red to pink.)

Chrysopa plorabunda Fitch (fig. 161)

1855 *Chrysopa plorabunda.* Fitch, First report, p. 88.
1861 *Chrysopa plorabunda.* Hagen, Synopsis Neuroptera N. Amer., p. 221.
1903 *Chrysopa plorabunda.* Banks, Trans. Amer. Ent. Soc., vol 29, p. 155.
1907 *Chrysopa plorabunda.* Banks, Cat. neurop. ins., p. 28.

Chrysopa plorabunda was found to be the most abundant species at Manhattan, Kansas, from early spring to late fall. It was found to be especially abundant in summer in alfalfa fields, in corn and sorghum fields, on willow, and on trees on which woolly aphids were plentiful. At Ithaca several specimens thought to be of this species were collected in a strawberry patch near a wood, but they were a darker green than the Kansas specimens. No eggs were deposited. At Charlottesville a third-instar larva was taken in sweeping a clover field on May 17, 1918.

The life history does not differ from those of the *oculata* and *rufilabris* groups. It may be outlined as follows: egg stage, 3 to 5 days; to first molt, 2 to 5 days; to second molt, 3 to 5 days; to spinning, 3 to 8 days; to emergence, 8 to 20 days.

Egg.—Elongate elliptical, light green in color with a decided yellow tinge; stalk hyaline. Stalked as in other species and deposited singly or in irregular groups. Length of egg, 0.87 mm.; greatest diameter, 0.37 mm.; length of stalk, 2.46 to 3.82 mm.

First-instar larva.—Head with two elongate, converging, longitudinal, black bands across dorsum, widening gradually to twice the width toward posterior border. Body predominately gray, with two broken and irregular, brown to reddish brown bands on each side of dorsal vessel, extending full length of body; lateral tubercles small, wholly gray in color, forming gray to yellowish gray border on each side of body. Legs with dark bands distally on femora, proximally and distally on tibiae, and distally on tarsi. Length, 2 mm.; width, 0.5 mm.

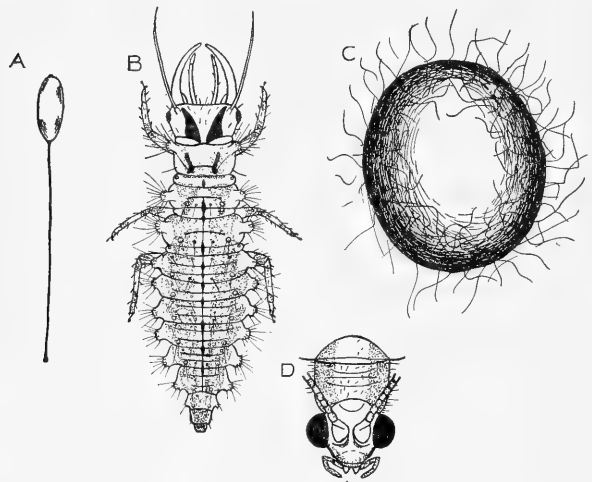


FIG. 161. CHRYSOPA FLORABUNDA

A, Egg, one day after deposition. B, Early third-instar larva. C, Cocoon. D, Cephalic view of head and dorsal view of prothorax of adult
(All x 8)

Second-instar larva.—Same as third instar, except for size. Head gray, with two longitudinal, converging, black or very dark brown stripes above, these broadening abruptly behind,. Thorax and abdomen each with a pair of amber brown or light brown spots, at anterior border on thorax, very irregular and broken up on abdomen; lateral tubercles rather small, wholly gray; eight or more small, colorless setae from each; a gray border on each side of abdomen. Legs dark, a grayish area around middle of femora and tibiae. Length of larva, 5 mm.; width at metathorax, 1.5 mm.

Third-instar larva.—Head predominately gray; two converging black or brownish black bands on dorsum of head, arising at inner side of bases of antennae, widening at base of head; jaws amber; palpi and antennae very light amber; eye spots jet black. Body predominately gray to slight yellowish gray, spotted with light red (near flesh color); anterior thoracic depressions black, each enveloped by a large, elongate, reddish spot; mesothorax with a pair of large triangular spots on each side of dorsal vessel; on remainder of thorax and abdomen, the spotting irregular and much broken up; lateral tubercles medium, wholly yellowish gray, forming a light border on each side of body; setae medium in length, colorless; dorsal papillae and tubercles all gray or yellowish gray; first abdominal segment with very small lateral tubercles, each bearing one or two very small setae. Legs predominately gray; smoky or somewhat blackish areas distally on femora, proximally and distally on tibiae; tarsi predominately black. Venter smoky to yellowish gray, with a reddish border of spots below lateral tubercles. Length of larva, 8 mm.; width, 2 mm.

(This larva resembles that of *C. rufilabris* except that the latter is lighter red in color and its color is more nearly solid. Also the lateral tubercles are smaller in *C. rufilabris*. *C. plorabunda* differs from *C. oculata* in its head markings and in having a complete gray or yellowish gray border to the body.)

Pupa.—Cocoon of white silk, somewhat transparent, almost as much so as in *C. rufilabris*. Length of cocoon, 3 mm.; diameter, 2.75 mm. (Pupae have head and body markings of adult to a large extent.)

Adult.—One of the most beautiful of our lacewings. Body yellowish green (chromium green); head somewhat more yellowish; a prominent greenish yellow (primrose yellow) stripe from head to end of abdomen; wings wholly green; a shining narrow band of reddish black from each eye to mouth; labrum and borders of dark band distinctly reddish.

(This species is distinct, but there appears to be almost a gradation to *C. harrisii*, *C. rufilabris*, and others closely related.)

Chrysopa sp.

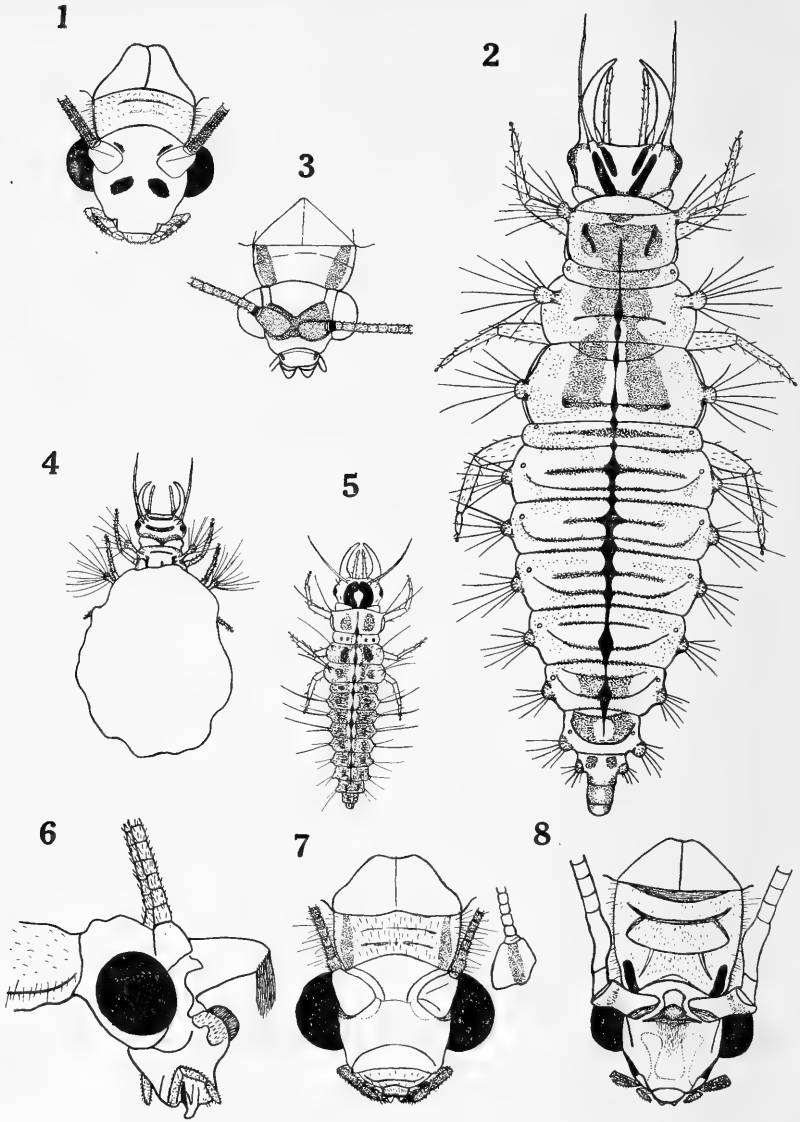
While sweeping goldenrod and asters, and in the Renwick marshes at Ithaca, the writer found two specimens of a gray larva. For some reason they failed to spin but curled up on the bottom of the vial. In a short time both were dead, and so the species is unknown. Since the larva is so distinctive, however, a brief description is included here. Only the third-instar larva was seen. It apparently belongs in the *quadripunctata* group.

Third-instar larva (Plate LXXXIV, 2).—Predominately gray. Head with four elongate black bands on dorsum, converging but not curved, inner pair about half as long and wide as outer pair. Prothorax largely gray; lateral tubercles small, wholly gray. Mesothorax with dark brown to blackish bands on each side of dorsal vessel, extending from prothorax to posterior part of metathorax and forming a saddle-shaped marking. Abdomen wholly gray, somewhat marked with brown or blackish along sutures; first segment without definite lateral tubercles; segments 2 to 5 alike, largely gray, marked with brown in middle and at each side; segments 6 to 8 darker, with prominent brown patches on each side of vessel; segments 9 and 10 still darker; all lateral tubercles relatively small and wholly gray, stalks short.

Chrysopa lineaticornis Fitch (Plate LXXVI, page 1307)

1855 *Chrysopa lineaticornis.* Fitch, First report, p. 91.
1861 *Chrysopa lineaticornis.* Hagen, Synopsis Neuroptera N. Amer., p. 215.
1903 *Chrysopa lineaticornis.* Banks, Trans. Amer. Ent. Soc., vol 29, p. 150.

Larvae of *Chrysopa lineaticornis* have been taken at Ithaca, where they were found on the lower branches and leaves of a linden in a densely shaded locality on August 27, 1916, and following days. Larvae were found also on underbrush near the linden. At Charlottesville, Virginia, they were taken many times during the summers of 1918 and 1919, mostly on the underbrush in woods, on honeysuckle vines, and on



SOME SPECIES OF CHRYSOPA AND MELEOMA

1, Head and prothorax of a female of Meleoma signoretti, x about 10¾
2, Mature larva of an undetermined species, Chrysopa sp. of text
3, Head and prothorax of an imago of a trash-carrying larva from Florida, probably a variety of Chrysopa lateralis
4, Dorsal view of third-instar larva of Chrysopa bimaculata
5, Probable first-instar larva of Meleoma signoretti, x about 10¾
6, Side view of head of male of Meleoma signoretti, showing protuberance, x about 10¾
7, Head and prothorax of Chrysopa lateralis
8, Head and prothorax of Meleoma slossonae, x about 10¾

oak and pine trees. They are readily found, for the little packet of debris moving over a green leaf is rather conspicuous. The best success in finding them was attained on early morning trips, since they appear to be more active at such hours. During the summer of 1918 they were most numerous during the month of September, but in 1919 they were most plentiful in the latter part of July, when all stages of the larvae were readily found. Adults were taken at Charlottesville practically all summer by beating oak branches in rather dense woods. The females have so far uniformly refused to oviposit in captivity. This species was never taken at lights.

Egg.—The egg of *C. lineaticornis* has not yet been seen, but singly deposited eggs of the usual stalked type are common on oak leaves and it is not unlikely that some may be of this species.

First-instar larva.—Conforms to description of third-instar larva except for size, number of setae on lateral tubercles, and dorsal head markings. Four convergent brown bands on dorsum of head; inner pair arising on inner side of antennae at bases of jaws, bending toward each other, and stopping together at about middle of head; outer pair arising between bases of antennae and eyes, extending parallel to inner pair, and stopping at posterior margin of head capsule; bands on posterior part of head, the invaginated part, very faint in color. Body gray, with some brownish or in some cases pinkish markings along sutures and in some specimens on each side of dorsal vessel; these markings, as well as dorsal vessel, inconspicuous; two setae from each lateral tubercle except meso- and metathoracic pairs, which bear three each; stalks of lateral tubercles unusually long. Length of larva, 2.5 mm.; width of head, 0.37 mm.; length of jaws, 0.32 mm.

(All first-instar larvae found, from the earliest to the end of the instar, have a well-defined packet of debris on their backs, identical with that of grown larvae except for size.)

Second-instar larva.—Like third instar with a few exceptions, chiefly as to size. Head grayish, with the two pairs of convergent brown bands as described above, these differing from those in the first instar in that they are broader and their color is a reddish brown, a considerably increased intensity of color; jaws amber, with a reddish brown line on outside of each extending to ocellar fields; a broad reddish brown band from ocellar fields to first subsegment of prothorax, on side of head. Body gray, but with more of the pinkish tinge at sutures and along dorsal vessel, this color being undoubtedly contributed by the viscera of the larva; a distinct brownish patch below each thoracic tubercle and covering proximal ends of coxae. Legs gray except distal ends of tarsi, which are black. Length of larva, 3.5 mm.; width of head, 0.55 mm.; length of jaws, 0.35 mm.

(The packet of debris is likewise a constant characteristic of this instar.)

Third-instar larva.—Head of usual shape, gray in color; two pairs of black or very dark brown bands on dorsum; inner pair arising at bases of jaws and curving toward each other, becoming parallel but not merging, and stopping at middle of head; outer pair arising between bases of antennae and ocellar fields and extending, nearly parallel to inner pair, to posterior side of head capsule, about midway the color becoming less intense and the sides of the bands somewhat irregular. (At the border of the prothorax in this species there is gen-

erally a beginning of a third pair of faint brownish bands, which extend toward the eyes but fuse with the long pair at the posterior end.) Eye spots jet black; jaws amber, with posterior half often dark; palpi and antennae translucent at bases but amber for the greater part. Body predominately gray; anterior subsegment of prothorax lighter gray than dominant color of head; second subsegment light gray in front, light brown behind; lateral tubercles very prominent, knobs at ends small and rounded, stalks unusually long; setae long and prominent, those on thoracic tubercles bending upward and arranged like a horizontal fan to support the packet, whitish to translucent; tubercles all gray. Entire dorsum whitish to delicate gray, main sutures darker. Thorax of normal length. Abdomen contracted and much broader than usual *oculata* type; width equal to that between tips of metathoracic tubercles; first abdominal tubercles not developed; tubercles 2 to 7 small, practically sessile; setae long, the longest ones extending fan-shaped and bending upward; abdominal sutures darkened. Sides of abdomen with a little brown extending full length of body. Tail prominent, somewhat translucent. Venter of thorax grayish to white, occasionally some pinkish due to color of internal tissues. Length of larva, 5.2 mm.; width of head, 0.8 mm.; length of jaws, 0.75 mm.

(All larvae taken have had a well-made packet of the type previously described.)

Pupa.—Cocoon spherical, slightly oblong, entirely of white silk closely woven. Length of cocoon, 3.64 mm.; diameter, 3.07 mm.

(The packet clings to one side of the cocoon and often nearly covers it, the only white silk then showing being on the under side next to the substratum. Larvae may fail to spin, but in such cases they may pupate outside a cocoon.)

Adult.—Specimens reared conform to description given by Banks (1903: 150), with the exception of very slight and probably inconsequential variations in color, largely due to age of specimen.

(Great difficulty was experienced in carrying the pupae through. Of approximately a hundred larvae, not more than a dozen have developed into adults. Midsummer rearings gave some success, but it was evident that the common garden aphids were not their natural food. All attempts at overwintering have failed.)

Chrysopa bimaculata McClendon (Plate LXXXIV)

1901 *Chrysopa bimaculata.* McClendon, Psyche, vol. 9, p. 215.
1903 *Chrysopa bimaculata.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 153.

Chrysopa bimaculata also is a trash carrier. The only specimens seen by the writer were larvae sent from the citrus groves of Florida through the kindness of Mr. Frank M. O'Byrne, of the Division of Nursery Inspection in the Florida Department of Agriculture. In habits the species is believed to be identical with *C. lateralis* and *C. lineaticornis*, except for distribution. Only the third-instar larva, the pupa, and the adult were seen.

Third-instar larva.—Differs from *C. lineaticornis* in head markings and in size. Head largely gray, with two brownish crossbands on dorsum, a narrow brown band connecting bases of jaws, another similar narrow band connecting

antennae, behind this band two dark brownish irregular patches reaching to prothorax. Body similar to larva of *C. lineaticornis*. Some variation in amount of brownish and black areas, and also in size. Specimens seen apparently on the average a little smaller than *C. lineaticornis*.

Pupa.—Same as in *C. lineaticornis*.

Adult.—Specimens conform to descriptions of type and to that of Banks (1903:153).

Chrysopa lateralis Guér.

Several adults of *Chrysopa lateralis* emerged from larvae sent to the writer from Florida. Unfortunately most of the larvae had spun cocoons by the time they arrived. But on comparing the old head capsule with the larvae that were seen, it appeared reasonably certain that the larvae of *C. lateralis* are almost identical with the same instars of *C. lineaticornis*. The only characteristic observed to be different was in the head markings. *C. lateralis* apparently has the two pairs of dorsal convergent dark brown to black bands. The inner pair arise inside the bases of the antennae, quickly converge, and extend as two convergent bands to a little beyond the middle of the head. The bands are widest in the anterior region and gradually become very narrow at the posterior border. The outer pair arise between the eyes and the bases of the antennae, and extend in a broad curve to the prothorax, almost parallel to the inner pair. On the outside of each of these bands is a large brownish spot of less intensity, making the outer pair of bands appear like a large elongate spot. The other head and body features, as far as known, are the same as are given for *C. lineaticornis*.

From one cocoon there emerged an adult which does not conform to any description yet seen, but it is close to *C. lateralis*. It differs in that the entire first segments of the antennae, and the antennal space on the head, are wholly bright red. But one specimen has yet been seen and there is some possibility that this is a variant.

Chrysopa cockerelli Banks

1903 *Chrysopa cockerelli*. Banks, Trans. Amer. Ent. Soc., vol. 29, p. 154.

About fifty larvae of the species *Chrysopa cockerelli* were first taken on the campus of the Kansas State Agricultural College on October 19, 1921, and following days, on the trunks of maple, linden, and dogwood trees. Several specimens were taken crawling over alfalfa under these trees. These larvae were fed for a time on aphids in the laboratory, but none of them spun cocoons. The larvae were divided into lots and placed in different situations for wintering. The percentage of fatality

was high, but five larvae overwintered successfully. In the summer of 1921, larvae of this species were taken during the latter part of June, early July, September, and October. Adults were taken only once, on August 19, 1921, when they were beaten from willows.

Egg.—All eggs of this species seen were stalked. Average length of five stalks, 4.9 mm. Egg elongate ellipsoidal, light yellowish green in color. Length, 0.8 mm.; greatest width, 0.46 mm. Taken on trunk of maple, June 16, 1921.

First-instar larva.—Head with two pairs of narrow brown bands dorsally; inner pair very narrow, arising at base of mandibles and extending slightly less than half the length of head; outer pair arising at base of antennae, extending posteriorly to prothorax, and doubling anteriorly to eyes; jaws very dark, almost black. Body predominately gray; internal organs visible, causing lighter-appearing areas over body; two setae each from all thoracic and abdominal tubercles except meso- and metathoracic, which bear three each; a row of small hooked setae on dorsum, on each segment from metathoracic to seventh abdominal inclusive. Larva normally carries a small packet of debris, though the usual long stalk of the thoracic tubercles and arched abdomen are not so pronounced as in other instars. Total length, 3.5 mm.; width at metathorax, 0.88 mm.; total length of head and jaws, 0.66 mm.

Second-instar larva.—Differs from third instar chiefly in size. Head and body markings the same as in third instar. Packet present in this instar also.

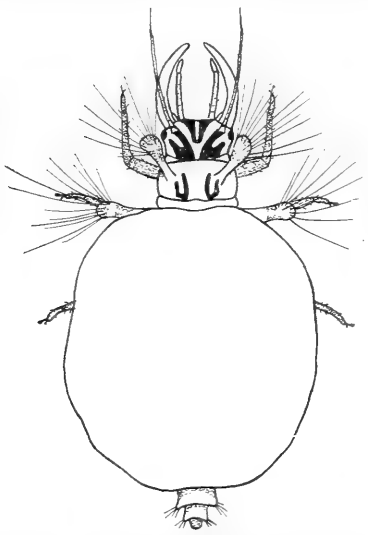


FIG. 162. FULLY GROWN THIRD-INSTAR LARVA OF CHRYSOPA COCKERELLI, WITH PACKET IN POSITION. DORSAL VIEW, X 10

Third-instar larva (fig. 162).—Head predominately smoky gray dorsally, with three pairs of black bands; inner pair converging behind, almost solid black between them or very dark except for a narrow gray area in middle line; middle pair arising between base of jaws and antennae and extending to prothorax, broadening behind and doubling back to eyes, forming the third pair; jaws amber-colored; antennae almost black, distinctly annulated. Body grayish to white in color, without black markings except along some sutures; prothoracic depressions prominent; lateral thoracic tubercles long and slender; prothoracic tubercles extending forward, setae long, stout, black, with prominent black bases; mesothoracic and metathoracic tubercles smaller and shorter than prothoracic, setae black. Legs very dark, almost black. Abdomen arched, bearing a packet of plant fibers, spider webbing, insect molts, and similar materials; from one to three more or less complete rows of microscopic setae with recurved tip on each segment from the metathoracic to the seventh abdominal segment inclusive; these setae longest on first, fifth, and sixth abdominal segments. Length, 6 mm.; greatest width, 3 mm.

Pupa.—Normally within white silken cocoons, the packet of larva often covering practically all of the cocoon. Pupae have not been found out of doors by the writer. Greatest diameter of cocoon, 2.9 mm.; least diameter, 2.3 mm.

Adult (fig 163).—The adults collected and reared conform rather closely to the original description by Banks (1903), but differ chiefly in the following minor characteristics: head largely ivory-colored, less commonly with a greenish tinge instead of yellowish; black lines to mouth not connecting, though the labrum is light brown; no red on anterior lobes of prothorax; cross-veinlets of wings very dark, the adjacent cells of many appearing smoky nearest the veins; length from head to tips of wings, 10 to 12 mm.

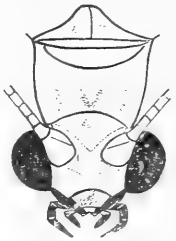


FIG. 163. HEAD AND PROTHORAX OF ADULT OF CHRYSOPA COCKERELLI, X 14

Other trash carriers

From a study of the cocoons in the collection of Chrysopidae in the Museum of Comparative Zoology at Cambridge, the following additional species are apparently trash carriers also: *Allochrysa parvula* Banks and *Leucochrysa floridana* Banks.

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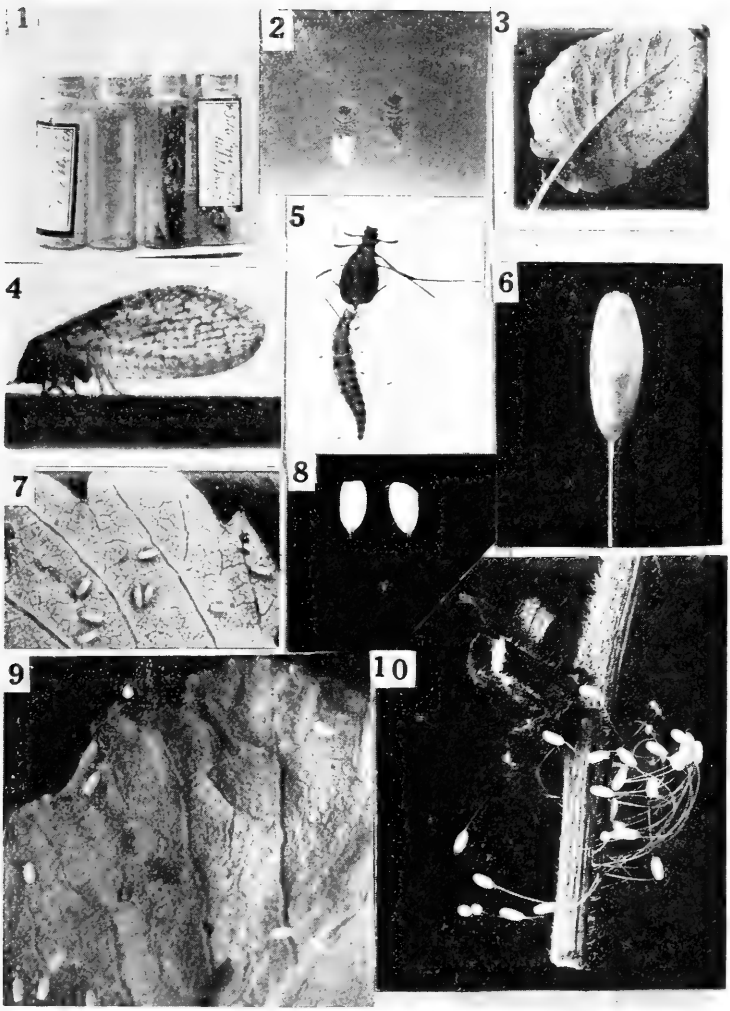


VARIOUS STAGES IN LIFE HISTORY OF SOME CHRYSOPIDS AND HEMEROBIIDS

1, Four dram vials plugged with cotton, as used in these rearings in the study of all stages. The cocoons may be seen

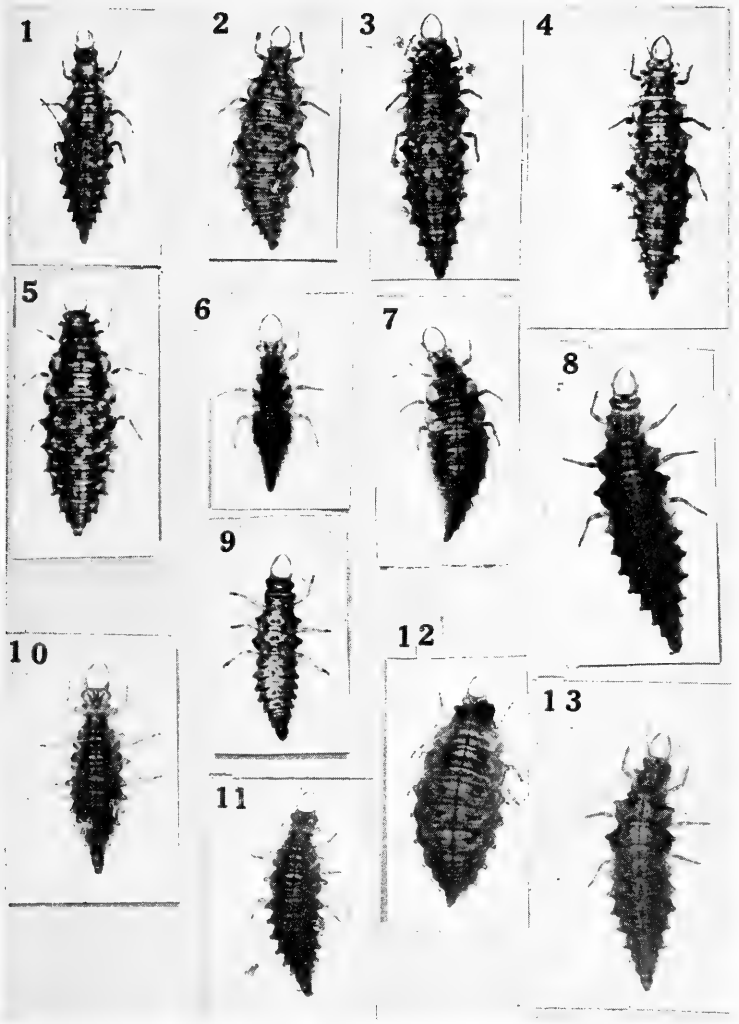
2, A larva of Chrysopa oculata in the final stage of hatching, and a newly hatched larva of the same species

3, Aphids on a leaf of cauliflower, as propagated in the laboratory for feeding chrysopid adults and larvae

4, Adult of a hemerobiid, Micromus posticus Walk., shown for comparison.

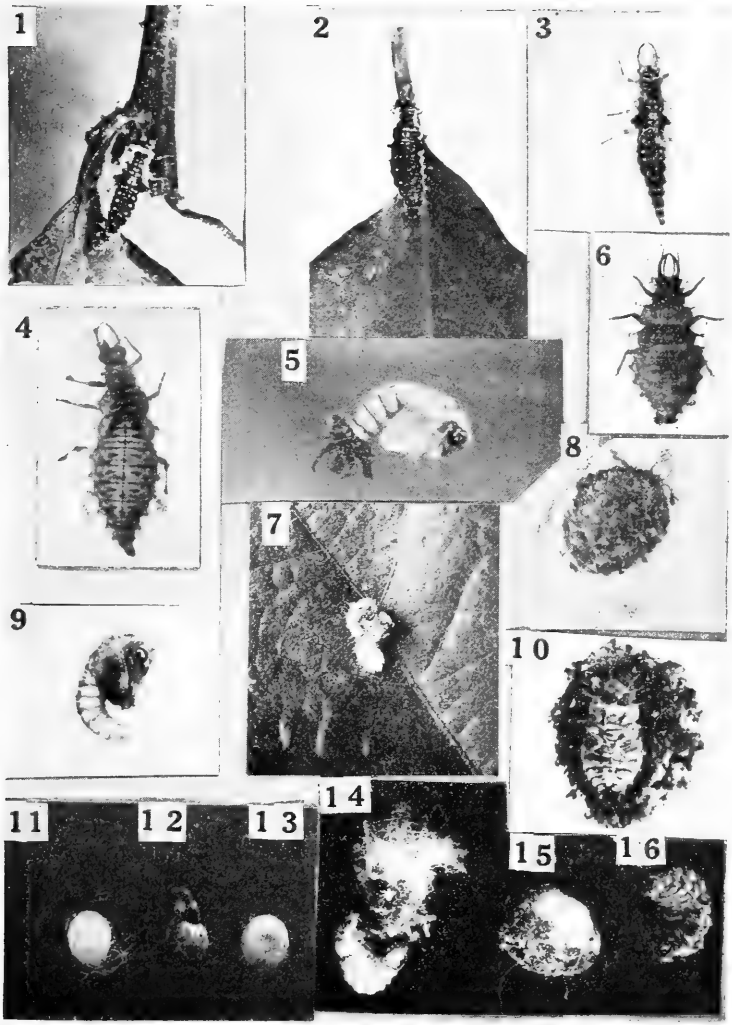
5, A grown larva of a hemerobiid, Hemerobius humuli, feeding on an aphid from an aster: shown for comparison with chrysopid larvae; x 3¾

6, An egg of Chrysopa oculata ready to hatch, showing outlines of the embryo; x 9¾. 7, Unstalked eggs of Micromus posticus deposited on a leaf in the laboratory, shown for comparison. 8, Two hatched eggs of Chrysopa nigricornis, showing the rent and the protruding embryonic molt; x 5¼. 9, Hatching eggs of C. oculata on a leaf; one larva may be seen on an egg shell, and others, newly hatched, on the leaf surface. 10, A tangled mass of eggs of C. nigricornis as deposited on a goldenrod stem in the laboratory



LARVAE OF VARIOUS SPECIES

1, Mature second-instar larva of Chrysopa oculata, showing the single head spot. 2, Third-instar larva of C. oculata, mature and about to pupate (the coloration is lighter than the average). 3, Mature third-instar larva of C. oculata with a few aphid skins adhering to lateral setae of thorax
4, Mature third-instar larva of C. oculata var. albicornis
5, Mature third-instar larva of C. oculata var. chlorophana
6, Second-instar larva of C. rufilabris, just molted. 7, Mature third-instar larva of C. rufilabris
8, Early third-instar larva of C. nigricornis, x 5¼
9, Ventral aspect of second-instar larva of C. oculata
10, Early third-instar larva of C. quadripunctata. 11, Grown third-instar larva of C. quadripunctata. 12, Mature larva of C. quadripunctata ready to spin, showing a mass of wax on prothorax from the goldenrod aphids
13, Mature larva of C. nigricornis, to be compared with no. 8
(All except no. 8 x 4½)



CHRYSOPID LARVAE AND PUPAE

1, Early third-instar larva of Chrysopa chi, x 4½. 2, Mature third-instar larva of C. chi. 3, Early third-instar larva of C. chi var. upsilon

4, A larva of unknown identity, designated as Chrysopa sp.

5, Pupa of C. oculata working the old larval skin over the end of the abdomen

6, Mature third-instar larva of C. lineaticornis, with packet of trash removed. 7, Larva of C. lineaticornis on an oak leaf, eating a pine mealy bug. 8, Larva of C. lineaticornis with packet in position; only the jaws of the larva showing

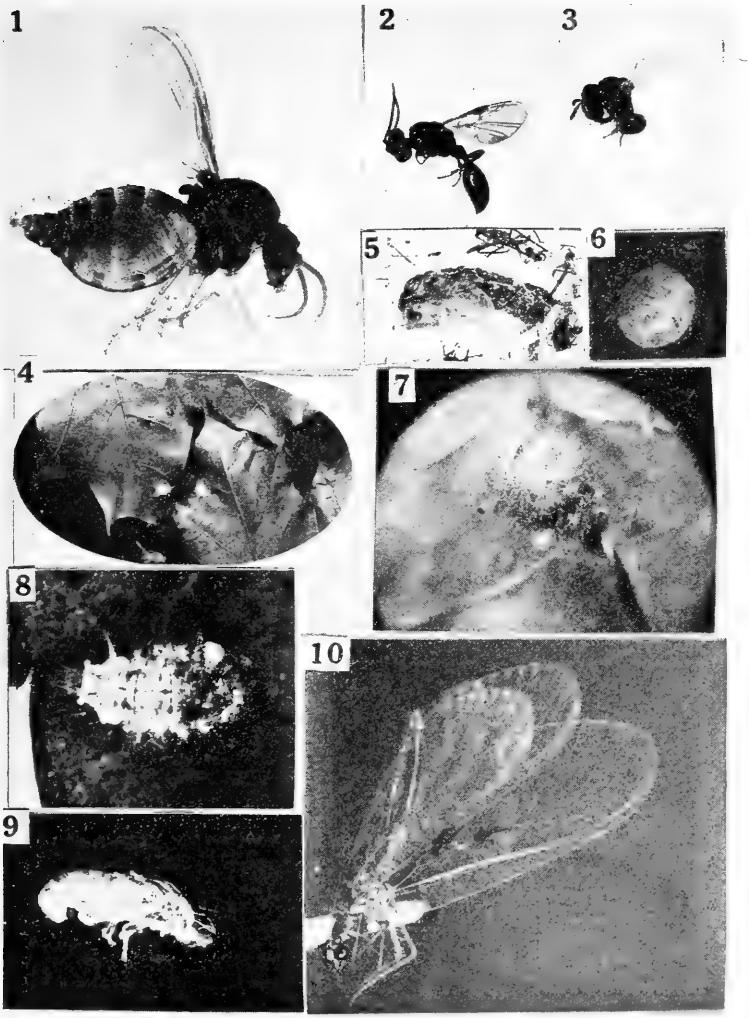
9, Pupa of C. chi in an advanced stage of development

10, Ventral aspect of third-instar larva of C. lineaticornis, showing relation of larva and packet

11, Cocoon of C. oculata, showing lid covering the opening through which the pupa emerged. 12, Pupa of C. oculata leaving cocoon. 13, Cocoon of wintering prepupa of C. oculata, showing flattened area where cocoon pressed against side of vial

14, Prepupa of C. lineaticornis beside larval packet; larva failed to spin a cocoon. 15, Normal cocoon of C. lineaticornis, showing old packet covering a part of cocoon

16, Prepupa of C. oculata, disturbed in spinning, curled up for transformation



VARIOUS STAGES IN LIFE HISTORY OF SOME CHRYSOPIDS AND THEIR PARASITES

1, Photomicrograph of the parasite Pseudoculicoides eques, from a balsam mount
2, Adult of the parasite Hemiteles areator subsp. tenellus, which emerged from a chrysopid cocoon
3, Adult of Perilampus sp., a pupal parasite
4, Cocoons, probably of Chrysopa nigricornis, found on the under side of maple leaves in summer; slightly reduced
5, A normal pupa of a hemerobiid, Micromus posticus, in its cocoon, shown for comparison
6, Wintering cocoon of Chrysopa nigricornis
7, Cocoon, probably of a trash carrier, found on under side of oak leaf at Charlottesville, Virginia, in September, 1918
8, Mature third-instar larva of C. quadripunctata, with trash over the abdomen; x 5¼
9, Pupal molt of C. oculata
10, Adult of C. oculata, with two parasites of the species Pseudoculicoides eques on a wing

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SOME RELATIONS OF ORGANIC MATTER IN SOILS

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The effect of lime on the organic matter in soils has been for some time one of the leading problems for investigation. The results that have been recorded, however, are not consistent. Some investigators have reported that there is a greater accumulation of organic matter in limed than in unlimed soil, while others have stated the contrary. This difference of opinion is not surprising when the methods of experimentation, the soil variations, and the climatic conditions are considered. There has been, however, too great a tendency to draw conclusions from unreliable data. In many cases, attempts have been made to study the effect of lime on the organic matter in soils without a knowledge of the composition of the soils before treatment.

In view of the many discrepancies in the reported results, the present experiment was designed to ascertain the effect of lime on the organic matter in soils under various treatments and cropping systems.

HISTORICAL

Wheeler and others (1899)[1] reported that lime decreased the percentage of humus in soils under continuous culture of cereals. They found also that there was an increase of roots and residual organic matter in limed grass plats as compared to those not limed.

Hess (1901) studied the effect of lime on some of the Pennsylvania soils. He stated that liming resulted in a diminution of the nitrogen.

Kossovich and Tretjakov (1902) stated that the addition of calcium carbonate to soil retarded the decomposition of organic matter.

Hartwell and Kellogg (1906) pointed out that the amount of humus in limed plats was less than that in unlimed plats. They stated also that the effect produced by lime upon the organic matter of a given soil was dependable to a considerable extent on the degree of acidity or of alkalinity of the soil.

[1]Dates in parenthesis refer to *References Cited*, page 25.

Pot experiments by Clausen (1906) conducted with clover and oats on sandy soil indicated that applications of lime resulted in a marked nitrogen hunger, especially during dry, hot weather and with non-leguminous crops.

Van Suchtelen (1910) found in laboratory experiments that soils treated with calcium oxide produced less carbon dioxide than did unlimed soils.

Alway and Trumbull (1910) say:

> In a comparison of 22 rotation plots no distinct relation has been found between the composition of the soil and the nature of the rotation. In a long cultivated field the till was found poorer in humus, nitrogen and organic carbon than the lacustral clay. The amounts of the above three constituents found in any of the plots depend more upon the relative proportions of the two types of soil occurring on the plots than upon the previous treatment.
>
> The longer the fields have been kept in grasses mown for hay, the less has been the change in composition of the soil. Continuous bare cultivation along tree rows has caused greater losses than the alternation of fallow and crop in the adjacent fields. The extreme loss of nitrogen, humus and organic carbon in 25 years is about one-third of the amounts originally present in the prairie.

Bradley (1912) conducted pot experiments from which he pointed out that the nitrogen loss was appreciably reduced by legumes.

Mooers, Hampton, and Hunter (1912) reported that the loss of nitrogen was appreciably greater on limed plats than on unlimed plats, and that the effect extended below the depth of plowing. These investigators stated also that there was an increase in percentage of humus on the unlimed sections.

McIntire (1913) writes:

> Burnt lime decreased the organic matter when applied alone and lessened the accumulation when applied with manure.
>
> Calcium sulphate and ground limestone increased organic matter.
>
> Each form of lime resulted in an increase of nitrogen content, gypsum, limestone, and burnt lime, being effective in the order named.

Lipman and Blair (1913) reported that in their experiments the limed plats had lost nitrogen to a greater extent than had the unlimed plats.

Gardner (1914) says: "Burnt lime appears to exhaust the humus in the soil more rapidly than ground limestone. Burnt lime with manure gave returns over manure alone. . . . It is desirable that the use of lime or limestone lead to larger supplies of organic matter in the soil."

Swanson (1915) reported results based on the chemical analyses of cultivated and uncultivated soils in seven representative counties in Kansas. He pointed out that the elements

carbon and nitrogen have disappeared from the cultivated soils to a larger extent than from the uncultivated soils. He showed that the cultivated soils had lost, in round numbers, from one-fifth to two-fifths of the nitrogen and from one-fourth to one-half of the organic matter.

Potter and Snyder (1916) stated that in a general way the total nitrogen determinations in their experiments showed that there was a smaller loss or a greater gain of nitrogen for the limed soils than for the corresponding unlimed soils.

Bear (1916) indicated that quicklime reduced the amount of carbon and of nitrogen in the soil.

Potter and Snyder, in a later experiment (1917), concluded that lime in the form of a carbonate, under the conditions of the experiment, appreciably enhanced the rate of decomposition of both original soil organic matter and the organic matter of stable manures, oats, and clover when added to the soil. They stated that two of the more important results of this were the increased availability of plant food and the more rapid depletion of the soil organic matter. They pointed out that the latter effect would be partially and perhaps entirely offset by the fact that with lime larger crops could be grown, which would add more organic matter as crop residue to the soil.

Breazeale (1917) found that calcium carbonate had a slight destructive action upon the organic matter of the soil.

Jensen (1918) stated that in most cases when lime was added to alfalfa in basins, greater increase in the humus content occurred than when alfalfa alone was used.

Christie and Martin (1918) state that it is evident from data considered that all soils do not react chemically with lime in the same manner.

Bizzell and Lyon (1918) write: "On Volusia silt loam addition of quicklime increased the amount of carbon dioxide in the soil air. This effect was noticed both on the cropped and uncropped tanks. On Dunkirk clay loam quicklime apparently produced no effect."

Swanson and Latshaw (1919) say:

> In the sub-humid section the fields cropped to grain lost one-fourth of the nitrogen as compared with the surface soil of the native sod. The alfalfa fields contain 5 per cent less nitrogen than the native sod, but 20 per cent more than the fields in grain. . . . .
>
> In the semi-arid section the cropped soil has lost one-fifth of the nitrogen as compared with the native sod. Alfalfa fields contained 15.7 per cent

more nitrogen than the soils in native sod, and 30 per cent more than the soils continuously cropped. . . . .

In the humid section, the cropped soils have lost 36 per cent of the organic carbon present in the virgin sod and those in alfalfa over 21 per cent.

Lipman and Blair (1920 a) summarized a series of experiments as follows:

Lime in the carbonate form was used on a loam soil at the rate of 1 ton per acre for the first 5 years and 2 tons for the second 5 years in a 5-year rotation of corn, oats, wheat and 2 years of timothy. No legume crops were introduced. Twenty plots with different nitrogen treatment were thus limed and twenty similar plots with parallel nitrogen treatment were left without lime.

The total yields of dry matter and of nitrogen for the 10-year period were essentially the same for the two sections.

Analyses of the soil made soon after the work was started and again at the end of each 5-year period showed that there was a loss of nitrogen from both the limed and unlimed sections. However, the loss from the limed section was distinctly greater than from the unlimed section.

Thus at the end of the 10-year period, there was a positive loss rather than gain from the use of lime.

From this work it would appear that the practice of using lime on light to medium heavy soils, *when leguminous crops are not grown* in the rotation, may be questionable. Under such conditions it is quite possible that a slightly acid reaction may be desirable to prevent the too rapid oxidation of organic matter.

The second five-years period showed a distinct loss in carbon from both series, but a greater loss from the limed than from the unlimed plats.

Lipman and Blair (1920 b) reported also a series of experiments which included rotations with legumes. They pointed out that during the ten years, the limed plots, with only slight exceptions, yielded distinctly larger crops and more total nitrogen than did the unlimed plots. In analyzing the soil they found that in a number of cases the limed plots contained more nitrogen than did the unlimed plots.

The same investigators (Lipman and Blair, 1921) reported the results of experiments in studying the losses of nitrogen and organic carbon from a loam soil (in cylinders with natural drainage) which for twenty years had been under a five-years rotation of corn, oats (two years), wheat, and timothy. They found that in most cases there was a general decline in the nitrogen and the organic carbon content. They pointed out that there was a lower nitrogen and organic carbon content in the limed soils than in the unlimed soils. They stated also that the legume green-manure crops tended to raise the nitrogen content.

It is quite impossible to make any direct comparison of

the literature cited, due to the variations in experimental methods and in representation of results. In fact, in many cases there are no data to substantiate the statements made. Furthermore, the making of comparisons of one plot with another on the assumption that the natural variation in fertility is gradual and uniform, is subject to severe criticism. It is likewise impossible to study the effect of lime on organic matter in soils without knowing the original composition of the soils. Also, conclusions drawn from computations based on analyses of soils taken adjacent to plats under treatment and assuming that the results obtained represent the original analyses of the treated plats, are questionable. However, the general conception expressed by the literature is that plats which have been limed contain less organic carbon and less nitrogen than do those which have not been limed. There are some exceptions. This conclusion is based on very limited experimental data.

EXPERIMENTAL

In the present investigation two series of field plats, each 1-100 acre in size, were used. The plats were sampled both before and after treatment. The soil was analyzed for inorganic carbon, organic carbon, and nitrogen.

The soil on these plats consists of glacial material reworked by streams and redeposited from glacial lakes (Lyon and Bizzell, 1918). Owing to its sedimentary origin it is comparatively free from stones. The soil has been classified by the United States Soil Survey as Dunkirk clay loam. It is a heavy, compact soil, and requires careful management. Its average mechanical analysis is as follows:

	First foot (per cent)	Second foot (per cent)
Fine gravel	0.40	0.13
Coarse sand	0.63	0.37
Medium sand	0.83	0.52
Fine sand	1.85	1.65
Very fine sand	12.90	11.27
Silt	60.83	53.95
Clay	22.63	32.72

The following chemical composition was determined by Lyon and Bizzell from representative samples:

Constituents determined	First foot (per cent)	Second foot (per cent)
Nitrogen (N)	0.134	0.062
Organic carbon (C)	1.190	0.300
Calcium oxide (CaO)	0.340	0.280
Magnesium oxide (MgO)	0.350	0.450
Potassium oxide (K_2O)	1.830	2.360
Sodium oxide (Na_2O)	0.860	0.860
Phosphoric anhydride (P_2O_5)	0.084	0.079
Sulfur trioxide (SO_3)	0.084	0.053
Carbon dioxide (CO_2)	0.030	0.020
Lime requirement* (CaO) in parts per million	1,222	1,285
Lime requirement (CaO) in pounds per acre foot†	4,454	4,918

* The Veitch method was used for the determination of lime requirement.
† Calculated from weight of soil as 3,645,000 pounds of dry soil per acre foot in the first foot of soil, and 3,827,500 pounds in the second foot.

SOIL SAMPLING

The plats in Series I were sampled both before and after the ten-years period. Soil samples were taken from each plat to a depth of four feet, each foot being kept separate. Six borings were made on each plat. The borings for the same foot were carefully mixed together and a 2-quart sample of each foot of each plat was retained. The soil samples were air-dried and placed in tightly sealed jars.

The plats in Series II were sampled before and after the eight-years period according to the following method: Each plat was divided into three parts—N (north), M (middle), and S (south). Each one of these sections was sampled as outlined for the plats in Series I.

Preparation of the sample

The air-dried soil was brought to a uniform condition by breaking up the soil lumps and carefully mixing. A composite sample was taken and was placed in a 1-millimeter sieve. All particles of the soil that did not pass through the 1-millimeter perforations were discarded. A composite sample was taken

from the 1-millimeter sample and was passed through a sieve having 100 meshes to an inch. In this case it was necessary to grind the soil in order to pass all of it through the perforations.

In the determinations of carbon the 100-mesh sample was used, while the determinations of nitrogen were made from the 1-millimeter sample. The use of the finer soil in the determination of carbon was based on the uncertainty of obtaining complete combustion with the coarser soil.

The determinations were made in duplicate. All duplicates having a wider discrepancy than 0.02 per cent of carbon and 0.01 per cent of nitrogen were discarded.

Total organic carbon

The total organic carbon was determined by the Parr Combustion Method, as described in Bulletin 107 (revised) of the United States Bureau of Chemistry, page 234.

Total nitrogen

The total nitrogen was determined by the Kjeldahl method. Ten grams of 1-millimeter soil was digested with 30 cubic centimeters of sulfuric acid (specific gravity 1.84) and 0.4 gram of cupric sulfate, in 500-cubic-centimeter Kjeldahl Pyrex flasks at low heat for twenty minutes. Ten grams of potassium sulfate was added and the digestion was continued for three hours. The residue was diluted to 350 cubic centimeters of water and transferred to an 800-cubic-centimeter Kjeldahl flask; from 80 to 90 cubic centimeters of alkali solution was added and the ammonia was distilled into 1-10 N sulfuric acid. The distillate, measuring about 200 cubic centimeters, was titrated with 1-10 N sodium hydroxide, two or three drops of methyl red solution being used as an indicator.

SERIES I

Soil treatment and cropping systems

The plats in Series I were under experimentation for a period of ten years, from 1910 to 1919. A statement of the soil

treatment of each plat, and of the cropping systems, is given in table 1:

TABLE 1. SOIL TREATMENT AND CROPPING SYSTEMS

Plat	Soil treatment		Cropping system
	Fertilizer	Lime	
7002	Farm manure	None	Rotation without legume
7008	Farm manure	Burnt lime	Rotation without legume
7003	Farm manure	None	No vegetation
7009	Farm manure	Burnt lime	No vegetation
7005	Farm manure	None	Rotation with legume
7011	Farm manure	Burnt lime	Rotation with legume
7006	Farm manure	None	Oats, grass nine years
7012	Farm manure	Burnt lime	Oats, grass nine years
7014	Farm manure and K_2SO_4	None	Rotation without legume
7015	Farm manure and K_2SO_4	Burnt lime	Rotation without legume

The applications of farm manure were made in 1910, 1914, and 1918. The three applications were each at the rate of 10 tons per acre, and were given to the plats that were never planted as well as to the cropped plats. The applications of potassium sulfate were made annually to plats 7014 and 7015 at the rate of 200 pounds per acre. In 1910 and 1915 burnt lime was applied to plats 7008, 7009, 7011, 7012, and 7015, at the rate of 3000 pounds per acre.

The rotation without legume consisted of corn, oats, wheat, and grass two years. In the rotation with legume, clover was grown with grass for two years in the first half of the ten-years period, and during the second half of the ten-years period a legume was grown each year as follows: in 1915, soybeans with corn; in 1916, peas with oats; in 1917, vetch with wheat; in 1918 and 1919, clover with grass.

Plats 7003 and 7009 were never planted to any crop, and all vegetation was prevented from growing on them by hoeing.

When corn was growing on the plats in rotation, the unplanted plats were hoed at the same time and in the same way as were the plats planted to corn; when other crops were growing on the planted plats, the unplanted plats were merely scraped with a hoe.

The mixtures of grasses used consisted of timothy, Kentucky blue grass, and redtop.

Results

Organic carbon and total nitrogen in plats before and after treatment

The results recorded in tables 2 and 3 represent the averages of duplicate determinations. The percentages of carbon and nitrogen before and after treatment are given, as well as the differences and the percentage of increase or decrease for the ten-years period. The total amounts of carbon and nitrogen added to the plats in manure, have been subtracted from the amounts of carbon and nitrogen determined on analysis after treatment.

The data show that in the first foot, in every case but one, the limed plats contained more organic carbon than did the unlimed plats. This is very significant in the plats kept in grass. Plat 7012, kept in grass and limed, shows an increase of 20.5 per cent of organic carbon in comparison to an increase of 14.5 per cent in plat 7006, which had the same treatment and cropping except that it was not limed. Plat 7002, cropped in rotation but not limed, shows a decrease of 24.5 per cent of organic carbon in comparison to a loss of 3.1 per cent in plat 7008, which had received lime. This difference is not attributed entirely to the lime. Plat 7002 was exposed to greater erosion and more complete drainage than was plat 7008. All plats in rotation show a decrease in organic carbon in the first foot, while there is a marked gain in organic carbon in the first foot in the plats kept permanently in grass.

The use of legumes in rotation did not materially affect the organic carbon content.

Plat 7009, which was kept bare, lost a marked percentage of organic carbon in the first foot.

The percentages of organic carbon in the second foot are

TABLE 2. PER CENT OF ORGANIC CARBON IN PLATS BEFORE AND AFTER TREATMENT. SERIES 1

Plat	Treatment	Before treatment		After treatment		Difference		Per cent of increase or decrease	
		First foot	Second foot	First foot	Second foot	First foot	Second foot	First foot	Second foot
7002	Crop rotation Manure	1.242	0.536	0.938	0.457	—0.304	—0.079	—24.5	—14.7
7008	Crop rotation Manure, lime	1.419	0.545	1.375	0.425	—0.044	—0.120	— 3.1	—22.0
7003	No vegetation Manure	....	0.420	1.027	0.348	....	—0.072	....	—17.1
7009	No vegetation Manure, lime	1.477	0.470	1.060	0.425	—0.417	—0.045	—28.2	— 9.6
7005	Crop rotation with legume Manure	....	0.420	1.040	0.365	....	—0.055	....	—13.1
7011	Crop rotation with legume Manure, lime	1.470	0.400	1.377	0.428	—0.093	+0.028	— 6.3	+ 7.0
7006	Grass Manure	1.286	0.500	1.473	0.545	+0.187	+0.045	+14.5	+ 9.0
7012	Grass Manure, lime	1.487	0.575	1.792	0.537	+0.305	—0.038	+20.5	— 6.6
7014	Crop rotation Manure, K_2SO_4	1.462	0.497	1.322	0.605	—0.140	+0.108	— 9.6	+21.7
7015	Crop rotation Manure, K_2SO_4, lime	1.405	0.537	1.309	0.528	—0.096	—0.009	— 6.8	1.7

TABLE 3. PER CENT OF TOTAL NITROGEN IN PLATS BEFORE AND AFTER TREATMENT. SERIES 1

Plat	Treatment	Before treatment		After treatment		Difference		Per cent of increase or decrease	
		First foot	Second foot	First foot	Second foot	First foot	Second foot	First foot	Second foot
7002	Crop rotation Manure	0.123	0.077	0.082	0.056	—0.041	—0.021	—33.3	—27.3
7008	Crop rotation Manure, lime	0.128	0.065	0.118	0.054	—0.010	—0.011	— 7.8	—16.9
7003	No vegetation Manure	....	0.077	0.109	0.057	....	—0.020	....	—26.0
7009	No vegetation Manure, lime	0.135	0.070	0.117	0.055	—0.018	—0.015	—13.3	—21.4
7005	Crop rotation with legume Manure	....	0.064	0.115	0.089	....	+0.025	....	+39.1
7011	Crop rotation with legume Manure, lime	0.145	0.069	0.139	0.089	—0.006	+0.020	— 4.1	+29.0
7006	Grass Manure	0.131	0.067	0.137	0.054	+0.006	—0.013	+ 4.6	—19.4
7012	Grass Manure, lime	0.159	0.071	0.161	0.064	+0.002	—0.007	+ 1.2	— 9.9
7014	Crop rotation Manure, K_2SO_4	0.152	0.065	0.125	0.077	—0.027	+0.012	—17.8	+18.5
7015	Crop rotation Manure, K_2SO_4, lime	0.142	0.081	0.125	0.090	—0.017	+0.009	—12.0	+11.1

less consistent than those in the first foot. This inconsistency may be accounted for by lack of soil uniformity.

The limed plats not only contained more organic carbon, but also gave higher yields, than the unlimed plats. The yields are expressed in graph form in figure 1 (page 17).

With one exception there was a greater percentage of nitrogen in the limed plats than in the unlimed plats. The plats in rotation all showed a loss of nitrogen in the first foot for the ten-years period, while the plats in grass increased in nitrogen. Plat 7009, which was kept bare, lost a marked percentage of nitrogen in the first foot. Plat 7011, on which the rotation included legumes, lost a smaller percentage of nitrogen in the first foot than did the plats in rotation without legumes.

These results are consistent with the results obtained on the lysimeter tanks (Lyon and Bizzell, 1918). The soil in the lysimeter tanks was obtained from the plats used in these experiments. It was found that the nitrogen in the drainage water from the lysimeter tanks was less where the tank soils had been kept in grass, than in a rotation. It was shown also that the tank soils kept bare lost more nitrogen than the cropped tank soils.

Ratio of carbon to nitrogen in plats before and after treatment

The ratios of carbon to nitrogen in plats before and after treatment are given in table 4. The data show the close relation between these two elements in the soils studied. The ratio was wider in the first foot of soil than in the second foot. The various treatments did not cause any constant change in the carbon-nitrogen ratio. The effect, if any, was too inconsistent to be considered significant.

The results compare favorably with those obtained by Hess (1901). He found that the ratio of carbon to nitrogen was not materially affected by the treatment applied. Dyer (1902) also reported that the carbon and nitrogen contents of the upper stratum of the soil were higher than those of the lower stratum, and that the ratio of carbon to nitrogen was wider in the upper stratum. Alway and McDole (1916) likewise found that the ratio of carbon to nitrogen was lower in the second foot than in the surface foot.

TABLE 4. RATIOS OF CARBON TO NITROGEN IN PLATS BEFORE AND AFTER TREATMENT. SERIES I

Plat	Treatment	Carbon-nitrogen ratios			
		Before treatment		After treatment	
		First foot	Second foot	First foot	Second foot
7002	Crop rotation Manure	10.1:1	6.9:1	11.4:1	8.2:1
7008	Crop rotation Manure, lime	11.1:1	8.4:1	11.7:1	7.9:1
7003	No vegetation Manure	.....	5.5:1	.....	6.2:1
7009	No vegetation Manure, lime	10.9:1	6.7:1	9.1:1	7.7:1
7005	Crop rotation with legumes Manure	.....	6.6:1	9.0:1	4.1:1
7011	Crop rotation with legumes Manure, lime	10.1:1	5.8:1	9.9:1	4.8:1
7006	Grass Manure	9.8:1	7.5:1	10.7:1	10.1:1
7012	Grass Manure, lime	9.4:1	8.1:1	11.6:1	8.4:1
7014	Crop rotation Manure, K_2SO_4	9.6:1	7.6:1	10.6:1	7.8:1
7015	Crop rotation Manure, K_2SO_4, lime	9.9:1	6.6:1	10.5:1	5.8:1

Removal of nitrogen from the soil in crops grown on the plats in Series I

The amounts of nitrogen removed in the crops were estimated and are recorded in table 5. The nitrogen is expressed in pounds per acre for the ten-years period.

TABLE 5. AMOUNT OF NITROGEN IN CROPS. SERIES I

Plat	Crop	Fertilizer	Burnt lime (pounds)	Nitrogen in crops (pounds per acre, total for ten years)
7002	Rotation without legume	Farm manure	0	684
7008	Rotation without legume	Farm manure	9,000	798
7005	Rotation with legume	Farm manure	0	817
7011	Rotation with legume	Farm manure	9,000	948
7006	Grass	Farm manure	0	325
7012	Grass	Farm manure	9,000	354
7014	Rotation without legume	Farm manure and K_2SO_4	0	844
7015	Rotation without legume	Farm manure and K_2SO_4	9,000	868

It appears that the nitrogen varies with different crops. The greatest removal of nitrogen was in the crops in rotation with legumes. The hay crops removed less than half the amounts of nitrogen estimated in the crops in rotation with legumes. These results are of extreme importance in considering the total nitrogen in the soils of these plats recorded in table 3, in which, as already stated, it is shown that the plats kept in grass increased in nitrogen in the first foot, while the plats in rotation with legumes and those in rotation without legumes decreased in nitrogen. The fact that less nitrogen was removed from the grass plats may aid in some degree in explaining these differences in percentages of nitrogen.

Total yields of crops on plats in Series I

The total yields of crops in Series I are represented in figure 1.

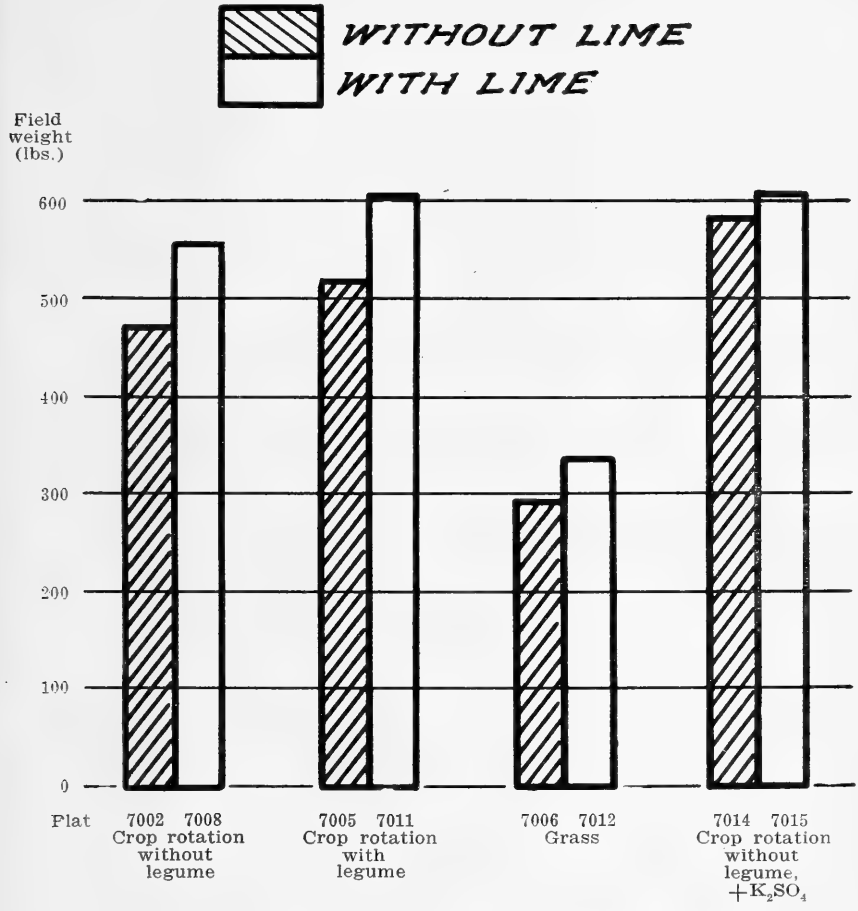

FIG. 1. TOTAL PLAT YIELDS FOR TEN-YEARS PERIODS, SERIES I

In every case there was an increase in crop yield on the limed plats over that on the unlimed plats. It seems logical to

assume that an increase in yield is associated with an increase in roots and residual organic matter, which may explain why the organic carbon and the nitrogen were generally higher in the limed plats than in the unlimed plats.

The total yields were less on the plats kept permanently in grass than on the plats in rotation with legumes or on those in rotation without legumes. It has already been pointed out, in tables 2 and 3, that the plats in rotation lost more organic carbon and nitrogen in the first foot than did the grass plats.

SERIES II

In order to obtain further information on the effect of treatment and cropping on the organic carbon and the nitrogen in soils, the plats in Series II, located adjacent to plats in Series I, were analyzed. These plats, as already stated, received approximately the same treatment as the plats in Series I, the only marked differences being that the plats of Series II were started one year later than the plats of Series I, and that they received only two applications of manure.

Only the first foot was analyzed, due to the failure of the second foot in Series I to show any consistent results of experimental value.

The results obtained are recorded in tables 6, 7, and 8. These tables are not discussed separately, due to their close correlation with the results of Series I.

The points emphasized in discussing the results of Series I may well be applied to Series II. However, the results in Series II are much more striking. The limed plats, as was found in Series I, show in general a higher percentage of organic carbon and of nitrogen than do the unlimed plats. The limed plats also gave higher yields than did the unlimed plats. There was a decrease in organic carbon and in nitrogen in the plats cropped under the rotation without legumes, with one exception.

The most interesting phase of these results is that the plats in rotation with legumes showed an increase in nitrogen. The percentages are very significant. Plats 7205 and 7211, in rotation with legumes, increased 4.2 and 6.7 per cent, respectively, in comparison to plats 7202 and 7208, in rotation without legumes, which decreased in nitrogen 12.2 and 7.1 per cent, respectively.

TABLE 6. PER CENT OF ORGANIC CARBON IN PLATS BEFORE AND AFTER TREATMENT. SERIES II

Plat	Treatment	Before treatment, First foot, Sections	Before treatment, First foot, Average	After treatment, First foot, Sections	After treatment, First foot, Average	Difference	Per cent of increase or decrease
7202	Crop rotation Manure	N 0.923 M 0.891 S 0.901	0.905	0.879 0.796 0.718	0.798	—0.017	—11.8
7208	Crop rotation Manure, lime	N 0.935 M 0.805 S 0.888	0.876	0.921 0.921 0.876	0.906	+0.030	+ 3.4
7203	No vegetation Manure	N 0.755 M 0.789 S 0.775	0.773	0.626 0.556 0.592	0.591	—0.182	—23.5
7209	No vegetation Manure, lime	N 0.797 M 0.788 S 0.731	0.772	0.821 0.719 0.592	0.711	—0.061	— 7.9
7205	Crop rotation with legume Manure	N 1.064 M 0.982 S 0.966	1.004	1.005 1.005 0.938	0.983	—0.021	— 2.1
7211	Crop rotation with legume Manure, lime	N 1.170 M 1.173 S 0.936	1.093	1.162 1.026 0.066	0.751	—0.342	—31.3
7206	Grass Manure	N 1.026 M 0.948 S 1.012	0.995	1.210 1.102 1.156	1.156	+0.161	+16.2
7212	Grass Manure, lime	N 1.088 M 1.080 S 0.874	1.014	1.387 1.228 1.028	1.214	+0.200	+19.7
7214	Crop rotation Manure, K_2SO_4	N 1.173 M 0.996 S 0.911	1.027	1.087 0.960 0.720	0.923	—0.104	—10.1
7215	Crop rotation Manure, K_2SO_4, lime	N 1.084 M 0.879 S 0.908	0.957	1.062 0.860 0.900	0.941	—0.016	— 1.7

TABLE 7. PER CENT OF TOTAL NITROGEN IN PLATS BEFORE AND AFTER TREATMENT. SERIES II

Plat	Treatment	Before treatment		After treatment		Difference	Per cent of increase or decrease
		First foot		First foot			
		Sections	Average	Sections	Average		
7202	Crop rotation Manure	N 0.120 M 0.115 S 0.110	0.115	0.098 0.105 0.099	0.101	—0.014	—12.2
7208	Crop rotation Manure, lime	N 0.120 M 0.112 S 0.103	0.112	0.109 0.109 0.094	0.104	—0.008	— 7.1
7203	No vegetation Manure	N 0.108 M 0.111 S 0.105	0.108	0.090 0.093 0.087	0.090	—0.018	—16.7
7209	No vegetation Manure, lime	N 0.111 M 0.111 S 0.100	0.107	0.099 0.096 0.079	0.091	—0.016	—15.0
7205	Crop rotation with legume Manure	N 0.122 M 0.128 S 0.103	0.118	0.124 0.119 0.126	0.123	+0.005	+ 4.2
7211	Crop rotation with legume Manure, lime	N 0.126 M 0.124 S 0.110	0.120	0.134 0.134 0.117	0.128	+0.008	+ 6.7
7206	Grass Manure	N 0.118 M 0.114 S 0.108	0.113	0.122 0.127 0.118	0.122	+0.009	+ 8.0
7212	Grass Manure, lime	N 0.129 M 0.115 S 0.112	0.119	0.140 0.124 0.112	0.125	+0.006	+ 5.0
7214	Crop rotation Manure, K_2SO_4	N 0.120 M 0.121 S 0.107	0.116	0.119 0.105 0.103	0.109	—0.007	— 6.0
7215	Crop rotation Manure, K_2SO_4, lime	N 0.113 M 0.111 S 0.101	0.108	0.115 0.101 0.105	0.107	-0.001	— 0.9

TABLE 8.. RATIOS OF CARBON TO NITROGEN IN PLATS BEFORE AND AFTER TREATMENT. SERIES II, FIRST FOOT OF SOIL

Plat	Treatment	Carbon-nitrogen ratios	
		Before treatment	After treatment
7202	Crop rotation Manure	7.9:1	7.9:1
7208	Crop rotation Manure, lime	7.8:1	8.7:1
7203	No vegetation Manure	7.2:1	6.6:1
7209	No vegetation Manure, lime	7.2:1	7.9:1
7205	Crop rotation with legume Manure	8.5:1	7.9:1
7211	Crop rotation with legume Manure, lime	9.1:1	8.5:1
7206	Grass Manure	8.8:1	9.5:1
7212	Grass Manure, lime	8.2:1	9.7:1
7214	Crop rotation Manure, K_2SO_4	8.9:1	8.5:1
7215	Crop rotation Manure, K_2SO_4, lime	8.9:1	8.8:1

The plats in grass showed a decided increase in organic carbon and in nitrogen.

The carbon-nitrogen ratios were lower than those in Series I.

Removal of nitrogen from the soil in crops grown on the plats in Series II

The amounts of nitrogen removed in the crops grown on the plats of Series II were estimated and are recorded in table 9. The nitrogen is expressed in pounds per acre.

The results compare favorably with those obtained in the study of the plats in Series I. In considering the nitrogen in the soils of the plats in rotation with legumes, as recorded in

TABLE 9. AMOUNT OF NITROGEN IN CROPS. SERIES II

Plat	Crop	Fertilizer	Burnt lime (pounds)	Nitrogen in crops (pounds per acre, total for eight years)
7202	Rotation without legume	Farm manure	0	555
7208	Rotation without legume	Farm manure	9,000	714
7205	Rotation with legume	Farm manure	0	690
7211	Rotation with legume	Farm manure	9,000	892
7206	Grass	Farm manure	0	312
7212	Grass	Farm manure	9,000	397
7214	Rotation without legume	Farm manure and K_2SO_4	0	652
7215	Rotation without legume	Farm manure and K_2SO_4	9,000	703

table 7, and that removed by the crops, the advantage from the growing of legumes is fully substantiated. The crops in rotation with legumes removed more nitrogen than did the crops in rotation without legumes. In this connection it is important to note also in table 7 that the plats in rotation with legumes contained more nitrogen than did the plats in rotation without legumes. While the plats kept in grass contained more nitrogen than did the plats in rotation, there is a marked difference in the amount of nitrogen removed by the hay crop as compared with the crops in rotation with legumes. The results show that the rotation with legumes used in these experiments supplied more nitrogen than did the rotation without legumes or the grass.

Total yields of crops on plats in Series II

The total yields of crops in Series II are represented in figure 2. The limed plats show a greater yield than the unlimed plats. This was true also of the plats in Series I. The total yields,

however, of both the limed and the unlimed plats in Series II are less than those in Series I. It may be pointed out here that the plats in Series II contained less organic carbon and nitrogen than the plats in Series I. This may indicate that there is some relation between organic carbon and nitrogen, and yields of crops.

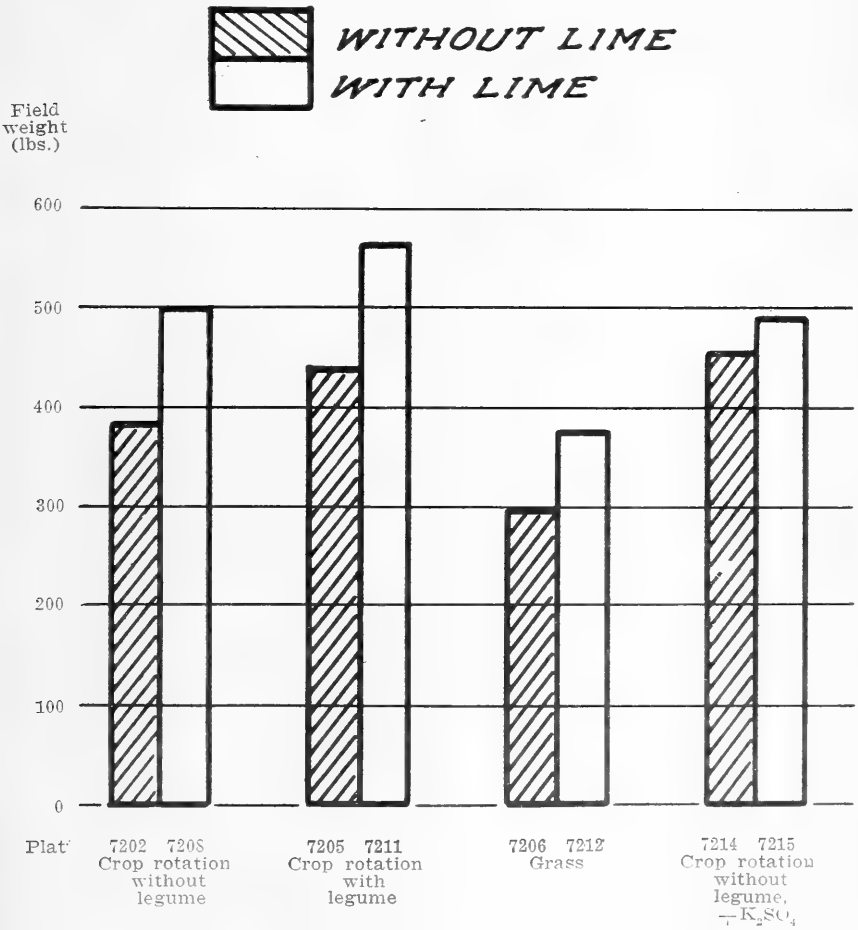

FIG 2. TOTAL PLAT YIELDS FOR EIGHT-YEARS PERIODS, SERIES II

The most important result shown in figures 1 and 2, as related to the present investigation, is the increase in yields of crops on the limed plats over those on the unlimed plats.

SUMMARY

A study of the effect of various treatments and cropping systems on the organic carbon and the nitrogen in soil is reported in this paper. The soil is classified as a Dunkirk clay loam. The plats were each 1/100 of an acre in size and were arranged in two series. The treatments included manure, potassium sulfate, and lime. The cropping consisted of a rotation without legumes, a rotation with legumes, and grass permanently. The experiment was conducted for periods of eight and ten years, respectively.

The plats were sampled for the first- and second-foot strata before and after treatment.

The organic carbon and the nitrogen were determined.

The results of the two series compared favorably.

In general the limed plats in both series contained more organic carbon and nitrogen than did the unlimed plats.

There was a decrease in organic carbon and in nitrogen at the end of the period of experimentation on the plats in rotation without legumes.

The plats kept in grass showed an increase in organic carbon and in nitrogen.

The plats in rotation with legumes contained more nitrogen than did the plats in rotation without legumes. The plats in rotation with legumes in Series II showed a marked increase in nitrogen. The increase was greater in the limed plats than in the unlimed plats. This fact seems to indicate that the legumes had some influence on the nitrogen content of the soil studied.

The organic carbon and the nitrogen were lower in the plats of Series II than in the plats of Series I.

The limed plats produced higher yields of crops than did the unlimed plats.

The plats in Series I gave higher yields of crops than did the plats in Series II.

The results suggest that there is some relation between organic carbon and nitrogen, and yields of crops.

The crops in rotation with legumes removed more nitrogen from the soil than did the crops in rotation without legumes.

The plats kept in grass lost less nitrogen in the crops than did the plats in rotation with legumes.

There is a close relation between the organic carbon and the nitrogen. The ratio is wider in the first foot of soil than in the second foot.

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THE NATURE AND REACTION OF WATER FROM HYDATHODES

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THE NATURE AND REACTION OF WATER FROM HYDATHODES

J. K. Wilson

In the process of growth and development, plants lose various parts of their structure. Root hairs are, relatively speaking, of short duration, and root-cap cells are gradually sloughed off; while pollen and other floral parts are soon lost. In addition to this loss of organic material, the plants return to the soil, by a gradual passing downward and outward through the root system, various inorganic and organic materials. These materials may be lost also through special organs, such as the nectaries or the hydathodes, the materials either falling off or being washed away by rain or dew.

In studying the effect that plants have on the growth of bacteria in soil, it became desirable, in order to throw light on the results that were being obtained, to make a study of the presence of certain materials in the exudate water of maize, oats, and timothy. This paper gives the results of the findings from this study, in so far as they bear on the broader investigation.

PREVIOUS STUDIES

An investigation somewhat similar to this was pursued by Berthelot and reported by Duchartre (1859). Four hundred cubic centimeters of guttation water was collected from Colocasia and evaporated to dryness. The residue contained potassium chloride, calcium carbonate, and a mucilaginous material. The last-named was completely soluble in all concentrations and produced a froth when boiled. When the dry residue was heated, it carbonized. It is concluded, however, that only the merest traces of organic and inorganic materials were found in this exudate, and that the concentration was about equal to that of distilled water.

Marloth (1887), in Egypt, collected the salts from the leaves and stems of Tamarix. The dry salts consisted of $CaCO_3$ 51.9 per cent, $MgSO_4H_2O$ 12 per cent, $MgCl_2$ 4.7 per cent, $MgHPO_4$ 3.2 per cent, NaCl 5.5 per cent, $NaNO_3$ 17.2 per cent, and Na_2CO_3 3.8 per cent.

Lepeschkin (1906) analyzed water from the secreting cells of a number of plants. In addition to a considerable number of inorganic substances, certain organic compounds were found. Glucose was secreted from *Vicia sativa* and *Polypodium aureum*, while basic oxalic acid was found in the water from *Lathyrus odoratus*.

The forms of nitrogen in plants were studied by Klein (1913). Guttation water was collected and examined, diphenylamine and nitron being used as reagents. Klein concluded that nitrates were not found in the exudate water from *Splitgerbera biloba*, *Fuchsia* sp., *Nicotiana silvestris*, *Tradescantia viridis*, *Tolmiaea Menziesii*, and *Zea Mays* seven weeks old, but were present in that from *Zea Mays* seedlings five days old. Also,

the exudate water from *Caladium antiquorum* gave a positive test with diphenylamine but no test with nitron.

Klein examined the first drop to appear on the leaves of *Boehmeria utilis* and *Fuchsia* sp., and found nitrates but no nitrites. The nitrites appeared in the exuded water after from six to eight hours, giving a strong test with Griess & Lunge reagents. After two days the nitrates had disappeared. Klein concludes that nitrites are found in the exuded water only after a partial reduction from the nitrates by bacteria or molds.

Lyon and Wilson (1921) grew plants whose roots were immersed in a sterile nutrient solution. They found in the solution surrounding the plant roots 535 milligrams of organic material, consisting in part of peroxidase and a reducing substance which were identified by color tests. This organic material had been liberated by the growing plant roots.

METHODS AND MATERIAL

It seemed desirable in the present study, because of the scarcity of material and the question of feasibility, to confine the investigation for the most part to a qualitative determination of various organic substances that may be present and readily detected in the exudate water. A number of tests were performed to determine some of the specific substances. Some of the tests were for the identification of specific organic compounds, while others were for inorganic substances. Klein considered that the nitrites which he found in the guttation water were produced from the nitrates by molds or bacteria. In order to avoid this complication, the various tests in this study were first performed on material collected from plants growing under non-sterile conditions, and then the technique was applied to exudate water collected from sterile plants.

The material for examination was collected from two sources. One was from maize grown in the greenhouse in soil. These plants were for the most part not more than three weeks old nor more than four inches high. They had from two to four blades when the water was collected. They were watered from an ordinary hose by spraying, but it is doubtful whether a great deal of this water was collected as exudate water. Exudate water was collected also from maize grown in water culture, and from the lawn grass, which was mainly blue grass, around the buildings on the campus.

The second source of material was from plants grown under sterile conditions. Among these plants were maize, timothy, and oats, grown from sterile seeds sown on a sterilized substratum.

From 20 to 30 cubic centimeters of the exudate water was collected in the course of an hour from maize which was growing under non-sterile conditions. This was taken from either the ends or the sides of the blades. It was used immediately in testing for certain substances which it might contain. In all probability it was somewhat more concentrated than when first exuded. All determinations were made, however, on the material as collected. Smaller amounts were collected from maize, oats, and timothy grown under sterile conditions.

PRESENCE OF CERTAIN INORGANIC MATERIALS IN WATER FROM HYDATHODES

Total solids

In making a determination of the inorganic as well as the organic materials in the exuded water, it was desirable to know the proportion of each. This was determined by evaporating 10 cubic centimeters of the water and weighing the residue both before and after igniting it. The material which was left after ignition was called *inorganic*, while that which was driven off on ignition was called *organic*. The results of three determinations are given in table 1:

TABLE 1. TOTAL SOLIDS AND ORGANIC MATTER IN WATER FROM HYDATHODES

Source of water	Total solids (parts per million)	Parts per million left after ignition	Parts per million lost on ignition
Non-sterile maize	1,030	280	750
Sterile timothy	573	377	196
Sterile timothy	220	90	130

These results indicate that there was a considerable variation in total solids of various collections; also, that the amount lost on ignition, which was called *organic matter*, varied from 130 to 750 parts per million. This variation may be due partly to the fact that plants of different ages were used.

Nitrites

To about 5 cubic centimeters of the exudate water from maize plants forty-three days old, the Griess reagents for the detection of nitrites were added. After a few minutes a pink color began to appear. At the end of twenty minutes the color was very pronounced but was much fainter than that of a standard which represented 0.0001 milligram of nitrites per cubic centimeter. The reagents did not give this test with distilled water.

In a second test, from three to four drops of an aqueous solution of 0.2 per cent sulfanilic acid was added to 4 cubic centimeters of the exudate water from maize plants forty-three days old, and the materials were mixed. From two to three drops of concentrated hydrochloric acid and an alcoholic diphenylamine solution was added to this mixture. When these were mixed, the red color that appeared was taken as an indication of nitrites. The reagents and distilled water did not give this test.

A third test for nitrites consisted in adding an alcoholic solution of alpha-naphthylamine and dilute hydrochloric acid to some of the exudate water, the development of a deep violet being considered a positive test for this constituent.

Exudate water from sterile maize, oats, and timothy, from eight to eighteen days old, gave these tests for nitrites.

Nitrates

To test for nitrates, 5 cubic centimeters of the exudate water from maize was evaporated to dryness, and to the residue was added 0.1 cubic

centimeter of phenoldisulphonic acid. The residue and acid was rubbed with a glass rod. After standing for ten minutes, 0.5 cubic centimeter of water was added, and then an excess of ammonia water 1:1. The development of a yellow color gave evidence of the presence of nitrates. This test was positive also with exudate water collected from maize eleven days old, oats nine days old, and timothy fourteen days old, growing under sterile conditions.

PRESENCE OF CERTAIN ORGANIC MATERIALS IN WATER FROM HYDATHODES

Reduction of methylene blue

The object of the first test for the presence of organic materials was to determine whether or not these materials would reduce methylene blue. The test was made in a white porcelain crucible. To 0.5 cubic centimeter of a normal solution of sodium hydroxide, enough methylene blue solution was added so that the bottom of the crucible was just visible. This mixture was then heated to the boiling point and some of the exudate water was added. With this procedure the color of the methylene blue entirely disappeared. On cooling, a color developed which had considerable red in it. This was considered a positive test for reducing substances. This reaction occurs when reducing sugars, and probably other substances, are present in the solution, and gives a positive test when 0.1 cubic centimeter of the solution being tested contains 0.0000039 milligram of glucose. This test was applied to exudate water collected under sterile conditions from maize, oats, and timothy, with positive results.

Sugar

The test for sugar was made according to the recommendations of Heriot (1920). It was positive with amounts as small as 0.004 per cent of sugar. To about 5 cubic centimeters of the water from maize, four drops of an alcoholic alpha-naphthol solution was added, and the two were thoroughly mixed. Concentrated sulfuric acid was added to form two layers. On standing, a bright red to deep violet color appeared at the surface of contact of the two liquids. The color became intense if the whole mixture was stirred and gently heated. Exudate water from sterile maize plants collected eleven days after planting, gave a positive test in less than two minutes. For exudate water collected from sterile oats nine days old, thirty minutes was required to produce the characteristic reaction. The test for sugar was positive with exudate water collected from sterile timothy plants varying in age from nine to eighteen days.

Enzymes

Catalase.— To about 9 cubic centimeters of the exudate water from maize, 0.5 cubic centimeter of hydrogen peroxide was added, and the solution was gently rotated to insure a thorough mixing. After a few minutes, bubbles began rising from the interior of the mixture. This action was accelerated when the mixture was warmed. No bubbles appeared in a similar mixture when distilled water and hydrogen peroxide were used. A similar determination with boiled exudate water gave

no bubbles. The bubbles were taken as an indication of the presence of catalase. The test was positive when made with exudate water collected from sterile oats, maize, and timothy.

Peroxidase.— In making the first test for peroxidase, 5 cubic centimeters of the exudate water from maize was placed in a test tube and about 0.1 cubic centimeter of hydrogen peroxide was added. The solution was mixed thoroughly and allowed to stand for from two to three minutes. After this interval a few drops of a five-per-cent phenol solution was added. If peroxidase was present, a browning of the solution occurred and after a time a precipitate settled to the bottom of the test tube. This reaction was very decisive. The browning began within ten seconds after the test was made, and was accompanied with a heavy brown precipitate. When a similar test was made using boiled exudate water, no reaction was obtained.

Tests with water from hydathodes of sterile maize eight days old and oats nine days old were also very decisive, while a test from timothy seven days old was negative and one from plants ten and thirteen days old was positive.

In a second test for peroxidase, two drops of hydrogen peroxide was added to about 3 cubic centimeters of the exudate water from maize, and the materials were mixed. In about one minute two drops of an alcoholic solution of guaiac was added. There was instantly a bluing of the guaiac, the blue color becoming intense. This did not occur if hydrogen peroxide was omitted or if the exudate water was boiled. This test was positive when made with exudate water collected from sterile maize, oats, and timothy.

Reductase.— Klein (1913) reports that no nitrites were found in water from the leaves of *Boehmeria utilis* and *Fuchsia* sp. when it was examined immediately after being excreted, but that they appeared after from six to eight hours, and that on longer standing ammonia developed. This loss of nitrates and subsequent appearance of nitrites and ammonia Klein ascribed to the action of molds and bacteria. It would seem that there are other possibilities in such a reduction. Nitrate-reducing enzymes are found in many plants, and, since exudate water has been in contact with living cells of the roots, the stems, and the leaves, it may have in it the power to reduce nitrates to nitrites and ammonia.

In a test to determine the presence of reductase, exudate water was collected from sterile timothy plants eighteen days old. The materials were used in the following proportions: 10 cubic centimeters of exudate, 2 cubic centimeters of a 50-per-cent solution of $NaNO_3$, 0.1 cubic centimeter of benzyl alcohol as an accelerator, 0.9 cubic centimeter of water. As a control, the 10 cubic centimeters of exudate was replaced by boiled exudate water. These materials were placed in a stoppered container and thoroughly mixed. The test and the control were kept at about 37° C. for forty-eight hours. At the end of this time the presence of nitrites was determined with the Griess reagents. It is presumed that these conditions were not favorable for bacterial growth.

A comparison of the solutions showed at least twice as much nitrite in the test as was found in the control. A somewhat similar test conducted for twenty-four hours, in which exudate water from sterile timothy

plants fourteen days old was used, also was positive though not so pronounced.

Tests of this character using water from maize fourteen and eighteen days old gave no increase in nitrites.

HYDROGEN ION CONCENTRATION OF WATER FROM HYDATHODES

It was pointed out by Haas (1920) that the hydrogen ion concentration in expressed sap of plants varies with the kind of plant, its stage of maturity, and the substratum on which it was grown. In this work it was desirable to know whether or not the exudate water of young plants would vary in hydrogen ion concentration in the same way. In order to throw light on this point, maize, oats, and timothy were grown under sterile conditions on the same kind of substratum, and timothy was grown also on five different kinds of substrata. The exudate water was removed from all the plants each day, and the hydrogen ion concentration was determined by the colorimetric method as published by Clark (1920), with the slight modification that the exudate water was placed in the wells of a spot plate and a small amount of indicator was added to each. The resulting colors were compared with Clark's color chart to determine their pH value. The findings are recorded in table 2:

TABLE 2. HYDROGEN ION CONCENTRATION OF EXUDATE WATER FROM MAIZE, OATS, AND TIMOTHY

(Plants seven days old at time of first collection)

Number of days after first collection	Maize	Oats	Timothy				
	Substratum*	Substratum*	Substratum *				
	1	1	1	2	3	4	5
	pH	pH	pH	pH	pH	pH	pH
0	8.2	6.3	6.6	6.8	7.0	6.8	6.8
1	6.2	6.4	6.2	6.8	7.0	6.2	6.6
2	6.4	6.6	6.2	6.6	6.6	6.4	6.2
3	6.4	7.0	6.4	5.8	6.6	6.8	6.6
4	5.2	6.4	5.6	5.6	6.4	6.8	7.2
5	5.2	6.6	6.4	6.4	6.4	.....	.....
6	5.3	6.6	6.2	6.2	6.2	.....	.....
7	6.4	6.4	6.2	6.2	.....	.....	.....
8	5.6	6.2	6.2	6.2	.....	.....	.....
9	5.0	5.2	6.2	7.4	.....	.....	.....
10	5.0	6.2	.....	.....	.....	.....	.....
11	5.4	6.4	.....	.....	.....	.....	.....
12	6.2	7.0	6.2	.....	.....	6.4	6.2
13	6.2	.....	.....	6.9	6.2	6.4	.....
14	6.6	.....	.....	.....	.....	.....	.....

* Substratum 1, full nutrient solution plus 1.5 per cent of agar to solidify; 2, distilled water and 1.5 per cent of agar to solidify; 3, soil with 30 per cent of full nutrient solution; 4, soil with 30 per cent of tap water; 5, soil with 30 per cent of distilled water.

It is observed that the first water exuded from the hydathodes of young maize, oats, and timothy plants as measured by the colorimetric method was approximately neutral and that as the plants became older the exuded water became more acid. In the case of maize this acidity increased

until it was about the same as that of the expressed sap of much older plants as determined by Haas. The reaction of the water from maize, timothy, and oats grown on a similar medium was not the same; the water from maize became considerably more acid than that from timothy or oats.

The hydrogen ion concentration of exuded water from timothy plants grown on a number of substrata suggests that with young plants the substratum makes very little if any difference in the hydrogen ion concentration. Probably the temperature and light conditions also are factors which operate to change the hydrogen ion concentration.

WATER FROM HYDATHODES AS A MEDIUM FOR BACTERIAL GROWTH

In a test to determine the extent of bacterial growth on water from hydathodes, 0.002 cubic centimeter of the exudate water from non-sterile maize was spread over 1 square centimeter of surface on a microscopic slide. After the water had spontaneously evaporated, the slide was passed through a flame and the residue was stained with Ziehl-Nielson carbolfuchsin. On examining this under the microscope it was observed that the natural contamination of the material as collected was less than 500 bacteria per cubic centimeter. Some of this exudate water was incubated for forty hours at room temperature, and the organisms then present were again determined. By that time such a heavy growth of bacteria had developed that the solution was very cloudy and an examination similar to the preceding showed more than 100,000,000 bacteria per cubic centimeter. A series of plates were made in order to determine the number present by this method. The plate counts showed more than 90,000,000 bacteria per cubic centimeter. A part of one colony was transferred to a slope and used subsequently in determining the growth of the organism in sterilized exudate water from lawn grass (table 3, H).

Water was collected from grass growing around the buildings on the campus. This was filtered through paper after the paper and the funnel had been thoroughly washed with distilled water and drained free of excess water. It was then distributed into carefully cleaned test tubes. sterilized, and inoculated with certain bacteria, the growth of which was determined. The result is given in table 3:

TABLE 3. GROWTH OF BACTERIA IN HYDATHODE WATER FROM GRASS ON CAMPUS LAWN

(Incubated at 25° C.)

Organism	Number of bacteria introduced per cc.	Bacteria per cc. 24 hours later	Bacteria per cc. 48 hours later
Nitrate reducer	19,500	44,500,000	103,000,000
Bacillus cereus	65	1,750,000	900,000
B. fluorescens	2,500	8,000,000	16,000,000
B. radicicola *	835	850,000	513,000
H †	19,000	87,000,000	146,000,000

* Host plant, *Trifolium repens.*
† H, organism isolated as natural contamination of water from hydathodes of corn.

The data show that there was a large increase in bacteria per cubic centimeter in twenty-four hours. A further increase is evident with three of the organisms after forty-eight hours. The falling-off in numbers with the other two organisms at the forty-eight-hour period is probably due to their having used all the organic material suitable for growth.

DISCUSSION OF RESULTS

The work herein reported shows that in the exudate water from the hydathodes of maize, oats, and timothy, both inorganic and organic materials were found. This was observed in the water from plants varying in age from eight to forty-three days. Color tests were made to identify some of the compounds. Since it is recognized that infection by molds or bacteria might change the composition of the water in a short time, the exudate water was collected from sterile and non-sterile plants for examination. The total solids were determined by evaporating a definite amount of the water and weighing the residue. The weight which was lost when the total solids were ignited was considered organic matter. No effort was made to determine what salts were present in the water other than nitrates and nitrites. This has been determined in a measure by other workers.

The organic materials that have been identified suggest that the exudate water may have a similar composition to that of the plant sap. This supposition is especially warranted by the fact that the exudate contains several enzymes which are known to be present within the cell, and that the hydrogen ion concentration is almost the same as that of expressed sap of similar plants as reported by Haas.

The identification of a substance capable of reducing nitrates to nitrites suggests that the nitrates which are taken up by the plant from the substratum are in part reduced to nitrites as they pass up through the plant tissues, and that this reduction may continue for some time after the water has been exuded through the hydathodes.

The organic material that is present in the water from hydathodes seems to be easily utilized by bacteria. Since under field conditions this water finds its way into the soil, it must serve similarly as a temporary source of food for soil organisms.

SUMMARY

The chief points brought out in this paper are the following:

Total solids in the water exuded through the hydathodes from maize plants growing under non-sterile conditions were as high as 1030 parts per million. The total solids in water from timothy plants which were growing in closed containers in the absence of microorganisms were much less, being in one case only 573 and in another only 220 parts per million. In all cases the total solids were more than half organic matter.

Reactions were obtained which indicated the presence of nitrites, nitrates, materials capable of reducing methylene blue, catalases, and peroxidases, in the exuded water from maize, oats, and timothy. Reductases were probably present in the water from timothy, but no reaction was observed to indicate their presence in the water from maize.

The exuded water from various plants was a good medium for the growth of bacteria. This was evidenced by an increase in the number of bacteria in inoculated water.

The hydrogen ion concentration of water from hydathodes of maize, oats, and timothy is nearly neutral when the water is exuded by young plants. The acidity increases as the plants become older, until a maximum is obtained.

CONCLUSION

From the data presented it seems logical to conclude that the water from hydathodes of plants contains both inorganic and organic materials, and that it is a good medium for the growth of certain soil organisms.

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